THE GENERA OF LACTUCEAE (COMPOSITAE) IN THE SOUTHEASTERN UNITED STATES [1]

BERYL SIMPSON VUILLEUMIER

Tribe LACTUCEAE Cassini, Jour. Phys. Chim. Hist. Nat. Arts **88**: 151. 1819 [2]

Herbs [or sometimes low shrubs or, exceptionally, small trees], mostly with milky juice and alternate or radical leaves. Heads homogamous. Florets perfect. Corolla with a strap-shaped, 5-toothed limb (ligule). Anthers sagittate or auriculate at the base, usually with small terminal appendages. Style branches short to long, narrowing toward the tip or obtuse; pollen-collecting hairs short to long. Achenes smooth to ribbed and rugose or muricate, often narrowed at the base and terminally beaked; pappus usually of one or more rows of simple or plumose bristles, rarely of scales or lacking. (Tribe Cichorieae Dumortier, Anal. Fam. Pl. 30. 1829; subfam. Cichorioideae Kitamura, Mem. Coll. Sci. Kyoto Univ. B. **13**: 4. 1937, *ibid.* **22**: 77. 1955; subfam. Lactucoideae Solbrig, Taxon **12**: 230. 1963; subfam. Liguliflorae auct., nom. inval.).

About 60–65 genera in five to eight subtribes, the center of diversity in the Mediterranean basin. About 60 species in 17 genera occur in the southeastern United States. Of these, only half are indigenous; the remainder are weedy species introduced primarily from southern Europe.

[1] Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB-6459X, principal investigator Carroll E. Wood, Jr.). This treatment follows the format established in the first paper of the series (Jour. Arnold Arb. **39**: 296–346. 1958.) The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on species included in this area, with additional data from other taxa between brackets. References that the author has not seen are marked by an asterisk.

I want to particularly thank C. E. Wood, Jr., not only for his advice, but for many additions and for an immense amount of editing. His efforts are especially evident in genera 1–8. Mistakes that remain are to be attributed solely to the author. I am also very grateful to K. L. Chambers for reading and adding to the section on *Krigia*, A. S. Tomb for reviewing the treatment of *Lygodesmia*, and D. K. Northington for numerous suggestions concerning *Pyrrhopappus*. N. Dunkly aided in checking and typing the bibliography and J. E. Hanhisalo typed the remainder of the manuscript. The illustration of *Cichorium* was drawn by L–V. Trautz and that of *Krigia* by K. S. Velmure.

[2] The tribes of the Compositae in the southeastern United States have been treated by Solbrig (Jour. Arnold Arb. **44**: 436–461, 1963). The reader should consult this work for additional information not included here (e.g., familial and tribal descriptions, notes, and references).

The tribe Lactuceae, the most distinctive of the Compositae, has been recognized as a taxonomic unit since A. L. de Jussieu (Gen. Pl. 168. 1789), and many authors still treat it as a subfamily (correctly Cichorioideae Kitamura) of the Compositae. Members of the tribe are easily distinguished by their homogamous heads of perfect flowers with 5-toothed ligulate corollas. Most species are also laticiferous.

There has been little historical agreement about the relationships of genera within the tribe, and numerous subtribal arrangements, the best known of which are those of Bentham & Hooker, Hoffmann, and Stebbins, have been proposed. Bentham & Hooker and Hoffmann considered certain morphological characters, including habit, pappus type, involucre, and receptacular bracts, to be of particular significance in delimiting subtribes. In 1953, Stebbins culminated almost 30 years of work on the Lactuceae with a classification of the tribe based on a completely different conceptual framework from that of any of his predecessors. Instead of trying to find "key" characters, he considered each genus individually and placed it with the genus to which it appeared to be most closely related. By clustering together a greater and greater number of genera and then drawing boundaries where there seemed to be significant discontinuities, he concluded that eight subtribes should be recognized. Although these subtribal groups are for the most part biologically meaningful and represent evolutionary units, they are difficult to characterize and Stebbins himself made no attempt to provide a key to the subtribes because he thought that it would have been impossible.

Stebbins's studies emphasized the value of karyotype, pollen morphology, shape of the style arms, geographical distribution, and ecology, in addition to the more usual morphological criteria. In 1966, Jeffrey, in a modification of Stebbins's scheme, pointed out the value of the size and shape of the pollen-collecting hairs on the style and style-arms and the type of pubescence of the exterior of the corolla tube as additional morphological characters. He concluded that the ligulate Compositae fall into 5 groups comprising 11 subgroups and 23 series, but he did not apply formal taxonomic nomenclature to these because he thought that further work is first necessary and because of his uncertainty of what status — tribal or subfamilial — should be given to the ligulate Compositae within the family. The genera of Lactuceae are here arranged in accordance with Stebbins's subtribal classification, but any modifications in relationships suggested by Jeffrey are noted under each genus.

In considering the Lactuceae as a whole, Stebbins concluded that *Dubyaea* and *Soroseris* come closest to representing the primitive members of the tribe. Data from floral and wood anatomy indicate that these genera are particularly unspecialized anatomically (Stebbins, Carlquist). Both genera have numerous supernumerary bundles in the ovary, a platform of bundles at the base of the ovule, and a lack of fusion between the ovarian and perianth bundles. These characters led Stebbins to postulate that *Dubyaea* was not far removed from an ancestral type that had a superior ovary and a unilocular ovary with two parietal ovules. Similar un-

specialized features have been found in a few members of the Senecioneae and the Mutisieae, but the Lactuceae do not seem to be more closely related to either of these tribes than to any other in the Compositae, and, in fact, Stebbins was unable to ally the Lactuceae with any other tribe in the family.

A compilation of cytological data from 53 genera of the Lactuceae by Stebbins, Jenkins, & Walters indicated that nine is the base number in the tribe. Throughout the tribe, as in the genus *Crepis* (see below), there seems to have been an evolutionary trend in karyotype morphology from large to small chromosomes and from median to subterminal centromeres.

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KEY TO THE GENERA OF LACTUCEAE IN THE SOUTHEASTERN UNITED STATES

A. Pappus of small scales, or of membranaceous scales and bristles, or absent.
  B. Pappus of numerous small truncate scales in one or two rows crowning the achenes; flowers sky blue (pink or white). . . . . 1. *Cichorium*.
  B. Pappus of bristles and scales, or of a single row of pointed scales, or absent; flowers yellow to orange.
    C. Pappus of simple bristles and scales, or of a single row of pointed scales. . . . . 2. *Krigia*.
    C. Pappus absent; annuals.
      D. Involucre of 2 series (8 erect bracts and a short outer series); leaves cauline with numerous heads paniculately arranged. . . . . 15. *Lapsana*.
      D. Involucre of a single series of bracts, cuplike in fruit; stems reduced, heads on slender peduncles. . . . . 2. *Krigia*.
A. Pappus of simple and/or plumose bristles in one or more series.
  E. Pappus of plumose bristles or of both plumose and simple bristles.
    F. Plants with a basal rosette of leaves, essentially scapose, leaves on flowering stems reduced; involucre of more than one series of bracts.
      G. Receptacle with a flat scale subtending each flower. . . . . 6. *Hypochoeris*.
      G. Receptacle naked, without scales. . . . . 7. *Leontodon*.
    F. Plants with leafy flowering stems.
      H. Leaves narrow, grass-like, the plant glabrous or with only floccose pubescence and glabrate with age; involucre of a single series of bracts; achenes slender-beaked. . . . . 5. *Tragopogon*.
      H. Leaves broad, rough-hairy with coarse multicellular hairs, these either pointed or bifurcate-hooked at tip; involucre of more than one series of bracts; achenes beakless. . . . . 8. *Picris*.
  E. Pappus of one or more series of simple setose and/or capillary hairs, never plumose.
    I. Achenes essentially cylindrical, columnar, fusiform, not strongly flattened.
      J. Leaves greatly reduced, usually to scales; stems stiff; heads with a slender involucre, 5–10-flowered; corolla rose-purple (rarely white); achenes long-tapering upward. . . . . 4. *Lygodesmia*.
      J. Leaves evident, in a basal rosette or cauline.
        K. Involucral bracts in a single series of ± equal height, sometimes with a tiny basal ring of small bracts; achenes beakless; flowers yellow.
          L. Achenes ± compressed, but not strongly flattened, with unequal ribbing; inflorescence of numerous small heads. . . . . 16. *Youngia*.
          L. Achenes ± cylindrical and equally ribbed; inflorescence of few to several medium-sized heads. . . . . 17. *Crepis*.

K. Involucral bracts in two distinct series or in several overlapping series.
  M. Achenes conspicuously beaked.
    N. Achenes not muricate, 4- or 5-ribbed; leafy-stemmed plants or sometimes scapose; pappus with a minute villous ring below. ..... 3. *Pyrrhopappus*.
    N. Achenes with 8 prominent ribs, strongly muricate above; scapose plants, the scapes 1-headed, hollow; pappus without a villous ring. ..... 14. *Taraxacum*.
  M. Achenes truncate, not beaked.
    O. Pappus white, composed of both straight bristles and soft, downlike ones; leaves glabrous, the margins with weak prickles; flowers yellow ..... 10. *Launaea*.
    O. Pappus of numerous capillary filaments; leaves never with marginal prickles.
      P. Inflorescence a branching raceme or panicle of drooping (rarely ascending) heads; involucre slender, cylindrical; flowers whitish, creamy, or pink; lower leaves often divided or deeply lobed. .... 12. *Prenanthes*.
      P. Inflorescence of 1 to many erect or ascending heads, mostly in corymbs or panicles; involucre campanulate; flowers yellow (orange-red in *H. aurantiacum*); leaves entire or only toothed. ..... 11. *Hieracium*.
I. Achenes flat or flattened, involucral bracts imbricated; stems mostly leafy.
  Q. Achenes beakless; pappus white, composed of straight bristles and fine down-like hairs intermixed; flowers yellow ..... 9. *Sonchus*.
  Q. Achenes beaked or short tapering at the apex; pappus white to tan; flowers yellow, purple, or blue. ..... 13. *Lactuca*.

Subtribe **Hyoseridinae** Lessing, Synopsis 127. 1832, "Hyoserideae."

1. **Cichorium** Linnaeus, Sp. Pl. 2: 813. 1753; Gen. Pl. ed. 5. 354. 1754.

Erect, caulescent perennial [biennial or annual] glabrous or pubescent herbs with petiolate, oblanceolate [lanceolate], parted or dentate [crisped] basal leaves, and alternate, lanceolate, dentate, clasping stem leaves becoming smaller and more entire upward along the stem. Heads homogamous, radiate, 1–3 in leaf axils, shortly pedunculate, or sessile, or terminal and solitary. Involucre of 2 series of bracts: the outer short, ovate to lanceolate, spreading; the inner much longer, lanceolate, rigid, upright, concave at the base where each clasps an achene; receptacle flat, naked. Corolla blue (pink or white), pubescent at top of corolla tube with slender hairs, except abaxially. Anthers with short basal auricles; pollen basically spherical and usually 3-pored and with an elaborate pattern of conical spines surmounting the structure (cf. Wodehouse, *plate 11, fig. 6*). Style branches long, thin, rounded at the apex. Achenes 5-angled, truncate at the apex, sometimes concave at the base, glabrous; pappus of one or two series of very short, flat, truncated scales forming a short crown atop the achene. LECTOTYPE SPECIES: *Cichorium Intybus*

L.; see Britton & Brown, Illus., Fl. No. U.S. ed. 2. 3: 305. 1913. (Origin of name disputed; according to Pliny from Egyptian and to Forsköl from Arabic, but according to Theophrastes and Dioscorides from Greek *kichorion*, of the fields, an appropriate derivation). — CHICORY.

A genus of some four to nine species usually considered to fall into two sections. Section CICHORIUM, including the majority of the species, all of which are native to Europe and the Mediterranean area, is distinguished by the many-floreted heads and glabrous plant bodies. Section ACANTHOPHYTON (Less.) DC. contains only a single species of middle Europe, Rhodes, and Cyprus, *C. spinosum L.*, which has spiny stems and heads with only six florets. Only the introduced *C. Intybus* L., chicory, chiccory, $2n = 18$, has become established in North America. This species, native to the mountains of northern Europe, now occurs in weedy habitats across southern Canada and in the United States from Maine to Washington state and south to California and Texas, in the west, and Georgia and Mississippi in the east.[3]

No serious attempt seems to have been made recently to analyze the extensive geographical variation present in *Chicorium Intybus*, and numerous infraspecific taxa have been recognized. Some polymorphic characters have been investigated and have been shown to be caused by the action of a single major gene (e.g., Rick has shown that the blue flower color is dominant over mauve (pink) in the Radichetta variety of chicory, and that long internodes are dominant to short).

Cichorium Intybus is most closely related to *C. Endivia* L., endive, $2n = 18$ (but some varieties with $2n = 36$). Bentham suggested that the two are conspecific, but recent biosystematic work has tended to confirm their more traditional treatment as distinct species. Rick found that the breeding systems of the two are different, *C. Intybus* being self-sterile and *C. Endiva* self-fertile. Nevertheless, natural hybrids are sometimes found and are easy to produce artificially. The close relationship of the two is shown by the complete bivalent pairing found in 209 out of 210 meiotic cells investigated from F_1 hybrids. Two cytogenetic differences were, however, discernible in the genomes of the parental varieties examined: one pair of chromosomes was unequal in length, indicating a deletion, and one pair formed bridges at meiosis in the hybrid, suggesting the presence of a translocation.

Because of its ready availability and ease of cultivation, *Cichorium Endivia* has been used as an experimental plant in numerous physiological studies. It is a winter annual and needs cold to stimulate maturation and flowering. Experiments have shown that only regular, frequent applications of gibberellin (but only at certain favorable temperatures) can duplicate the long-term effects of cold. Cold apparently stimulates the production of a substance similar to gibberellin.

[3] Small (p. 1490) lists this species as occurring in Florida, but I can find no specimen, nor a citation of one, from any locality south of Georgia and Mississippi, although Ledin includes it as a garden plant in southern Florida.

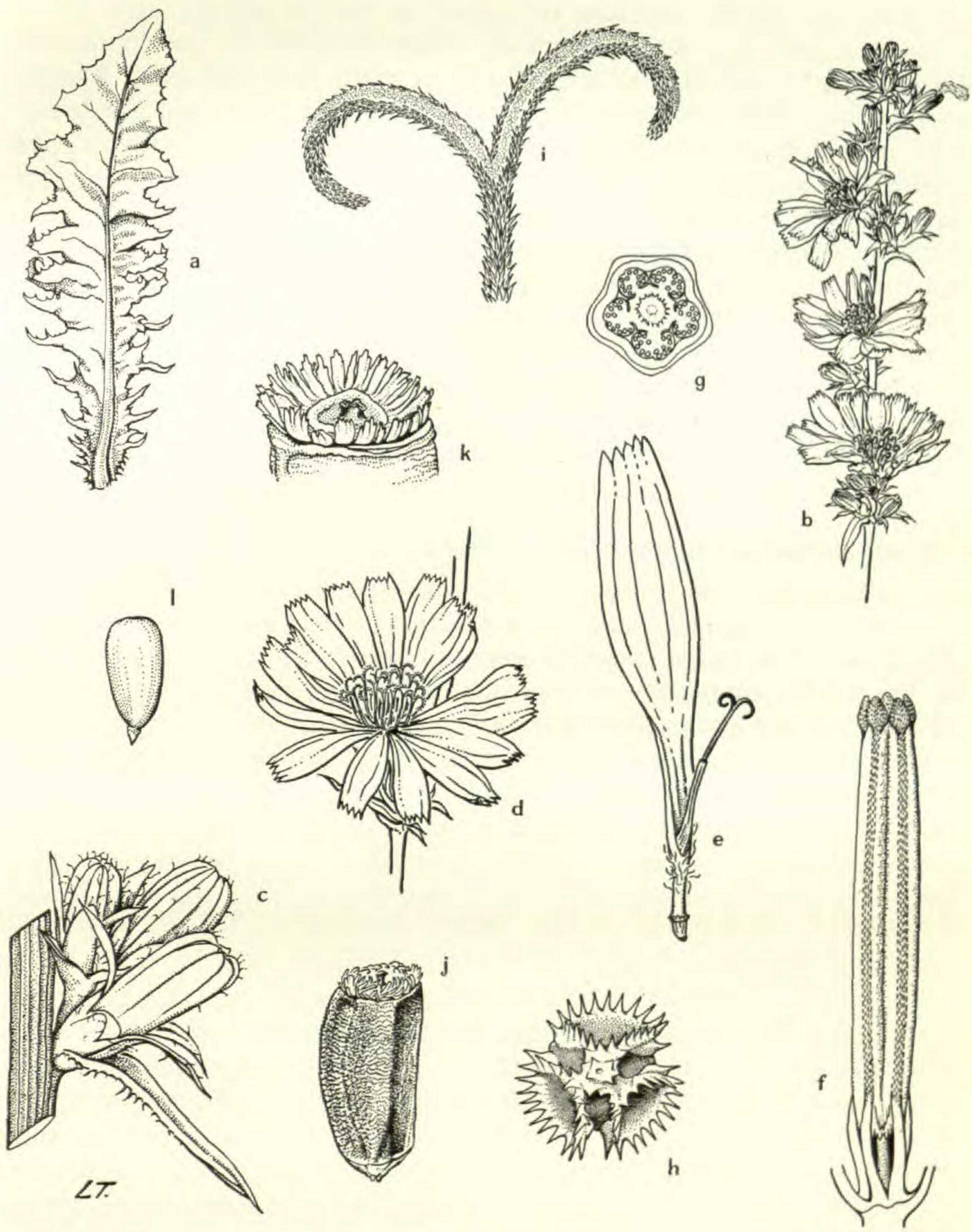

FIGURE 1. **Cichorium.** a–l, *C. Intybus*: a, basal leaf, × 1/4; b, upper part of flowering stem, × 1/2; c, glomerule of heads in axil of bract, lowermost head after anthesis, the corollas fallen — note two series of involucral bracts, × 2; d, head at anthesis, × 1; e, flower, × 4; f, androecium from bud just before anthesis, style not shown — note apical and basal appendages, × 8; g, cross section of flower bud just before anthesis, showing corolla, five coherent anthers (locules of adjacent anthers confluent), and style with pollen-collecting hairs, × 20; h, pollen grain in polar view, diameter ca. 40 μm. (after Wodehouse); i, upper part of style with stigmas, × 15; j, achene in lateral view, abaxial surface to left, × 12; k, detail of pappus of scales, from adaxial side of achene — note persistent style base, × 20; l, seed with papery seed coat, oriented as in achene, cotyledons of embryo parallel with page, × 8.

Cichorium Intybus has long been used in Europe and northern Africa as both a medicinal and food plant. Pliny recorded its use in ancient Egypt as a "friend of the liver." Extracts made from the roots, flowers, and achenes have been used as diuretics and laxatives, and the leaves have been applied externally to help heal infections. Recent studies have shown that a compound that has positive bacteriostatic effects is present in roasted or dried roots. The chemical, isolated by chromatography, effectively inhibits numerous microörganisms and is possibly responsible for the efficacy of extracts of chicory in treating gall-bladder and kidney and infections. Although not positively identified, comparative chemical reactions suggest that the principle may be a sesquiterpene.

Ground, roasted chicory root has been used for making a beverage since the late eighteenth century, and is today frequently substituted for, or mixed with, coffee to which it imparts a bitter taste. The stimulatory effects of chicory are probably due to the glucoside chicorin ($C_{32}H_{34}O_{10}$).

Both *Cichorium Intybus* and *C. Endivia* are cultivated as greens that are eaten either raw or cooked, and considerable confusion stems from popular names applied to the various forms of the two species. In Great Britain all forms of the two are known as *chicory* and *endive*, respectively; in the United States the wild naturalized *C. Intybus* and its root are *chicory*, but the blanched leafy form imported from Belgium (where it is known as *witloof, barbe-de-bouc, or chicorée de Bruxelles*) is *Belgian endive*; the curly-leaved form of *C. Endivia* is *chicory*, while the flat-leaved form is *endive* or *escarole*. In France, the wild plant and root of *C. Intybus* are *chicorée, chicorée sauvage*, or *barbe de capucin*; the blanched, leafy cultivated forms are *endive* or *endive de Belgique*; the curly-leaved forms of *C. Endivia* are *endive frisée*, and the flat-leaved forms are *escarole, scarole*, or *scariole*.

Generically, *Cichorium* is rather isolated within the subtribe Hyoseridinae Less., but on morphological grounds it appears to belong with *Hymenonema* Cass. and *Catananche* L. (cf. Cassini and Stebbins), two small genera also native to the Mediterranean area. Jeffrey also considered it isolated and treated it as the only member of his *Cichorium*-subgroup, of the *Cichorium*-group that includes, among others, *Dubyaea, Prenanthes, Crepis, Taraxacum, Chondrilla*, and *Launaea*. In his classification, *Hymenonema* and *Catananche* are members of the *Tolpis*-group.

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Subtribe **Microseridinae** Stebbins in Solbrig, Taxon **12**: 234. 1963.

2. **Krigia** Schreber, Linn. Gen. Pl. **2**: 532. 1791, nom. cons.

Low annual or perennial herbs, sometimes with a short perennial caudex or a small underground tuber. Leaves basal or alternate, petiolate, simple, entire, toothed, or pinnately to lyrately lobed; cauline leaves sometimes sessile. Flowering stems caulescent or scapose, monocephalous or branched with the heads on long peduncles. Involucre of 1 or 2 series of narrow equal-sized bracts reflexed at maturity or becoming somewhat thickened and standing upright to form a cup surrounding the achenes; receptacle flat to slightly convex, naked or fimbrillate. Florets perfect. Corolla ligulate, monochromatic, yellow to orange. Anthers with short terminal appendages and small, inconspicuous tails. Style branches obovate, short, flat. Achenes cylindrical or angled, truncate at apex and tapering at base, 10–15-ribbed, glabrous or pubescent; pappus double, the inner pappus capillary, the outer of short, flattened scales, or pappus of a few short scales, or reduced to a minute scaly crown, or altogether absent. (Including *Apogon* Ell., *Cymbia* (Torrey & Gray) Standley, *Cynthia* D. Don [nom. superfluum], *Serinia* Raf., *Troximon* Gaertner.) TYPE SPECIES: *K. virginica* (L.) Willd. (*Tragopogon virginicum* L.), typus cons. (Named for David Krieg, a German physician born in the 17th century, who was among the first plant collectors in Maryland.) — DWARF DANDELIONS.

A genus of seven species in two sections (Shinners) endemic to temperate North America, six of the species occurring in the southeastern United States. The species are rather sharply defined and often can be distinguished on the basis of the pappus alone. Numerous authors have assigned the species to two or three genera, but the inclusion of all in a single genus (cf. Stebbins, Shinners, Chambers) seems more meaningful biologically in view of the great similarity in structure of florets, achenes, involucre, and foliage.

Section KRIGIA (sect. *Eucynthia* (DC.) Shinners, sect. *Eukrigia* Torrey

& Gray, subg. *Cynthia* (D. Don) Gray; *Troximon* Gaertner; *Cynthia* D. Don, *Cynthia* sect. *Adopogon* DC.) includes four species, all with heads with 8–16 involucral bracts that are reflexed at maturity. *Krigia Dandelion* (L.) Nutt., $2n = 59$ (probably 60), derives its vernacular name, potato-dandelion, from the small ovoid to spherical tuber some 0.5–6 cm. underground from which the caudex of the season grows. Individual plants produce at or near the surface of the ground slender stolons that develop at their tips either rosettes of leaves or tubers (of two internodes; cf. Holm, 1891) that produce a leafy sprout the following season. The heads are solitary on naked scapes, and the pappus is composed of 25–45 unequal bristles 5–8 mm. long and 10 oblong-lanceolate scales. The plant is distributed mainly on the Coastal Plain from Florida to southeastern Texas, northward to New Jersey, Kentucky, Illinois, Missouri, and Kansas. Also perennial but lacking tubers and having more or less leafy stems, *K. montana* (Michx.) Nutt., $2n = 20$, occurs mostly on wet, open rocks in the mountains of western North Carolina, eastern Tennessee, and northern Georgia. The pappus is composed of 15–25 bristles 4.5–6 mm. long and 5 oblong-oval scales. A third perennial, *K. biflora* (Walter) Blake, $2n = 10, 20$, is widely distributed from North Carolina and Georgia to Arkansas, northward to Massachusetts and Minnesota, and has remarkable disjunct occurrences in Colorado, New Mexico, and Arizona. The stem leaves are few and reduced, the flowering peduncles come from the axils of reduced leafy bracts, and the pappus is composed of 20–40 unequal bristles 4.5–5.5 mm. long and of about 10 oblong-ovate or oblong-lanceolate scales. The annual *K. virginica*, $2n = 10$, is the most widely distributed of the species, occurring from Florida to Texas, north to Maine, Vermont, Ontario, Michigan, Wisconsin, and Iowa. The involucral bracts are much shorter than in the preceding species, and the reduced pappus is composed of five bristles 4.5–5 mm. long, alternating with five truncate scales.

The three annual species composing section CYMBIA Torrey & Gray (sect. *Bellidion* Scheele; *Apogon* Ell., *Cymbia* (Torrey & Gray) Standley, *Serinia* Raf.) have heads with 4–10 involucral bracts that remain upright, the involucre being more or less cuplike at maturity. It seems likely that the involucre of these plants may function like a splash-cup in the dispersal of the achenes, which either lack a pappus or have a greatly reduced one. In *Krigia occidentalis* Nutt. the pappus is composed of five bristles only 1.2–2 mm. long and five scales 0.4–0.6 mm. long, while in both *K. cespitosa* (Raf.) K. L. Chambers (*K. oppositifolia*, nom. invalidum),[4] $2n = 8$, and *K. gracilis* (DC.) Shinners the pappus is either com-

[4] **Krigia cespitosa** (Raf.) K. L. Chambers, comb. nov. *Serinia cespitosa* Raf. Florula Ludoviciana 149. 1817. *Krigia ? oppositifolia* Raf. *loc. cit.* 57, nomen invalidum.

On page 57 of his *Florula Ludoviciana* Rafinesque gave the name of this plant as *Krigia ? oppositifolia* Raf., but under "Additions" on page 149 of the same work he wrote, "Sp. 175. *Krigia oppositifolia*, must rather be called *Serinia cespitosa* Raf. The genus *Serinia* differs from *Krigia* by the naked seeds; the name means *small chicory*." Shinners (*Wrightia* 1: 202. 1947) and Merrill (*Index Rafinesquianus*, 241. 1949) treated *Serinia cespitosa* as a substitute name (nomen novum) for *Krigia oppositifolia*, as

pletely lacking or is reduced to a minute scaly crown up to 0.2 mm. long. The involucres of *K. cespitosa* are only 3–4.3 mm. tall in flower, and the corollas are only 2–4 mm. long, while those of *K. gracilis* are 5.3–8.3 and 5–10 mm., respectively. *Krigia occidentalis* occurs from southeastern and eastern Texas westward to the plains region of Texas, northward to Oklahoma, Arkansas, and southwestern Missouri; *K. cespitosa* in spite of its lack of pappus, is widely distributed from Florida and Texas, northward to North Carolina, Tennessee, southern Illinois, Arkansas, Kansas, and Oklahoma; and *K. gracilis* is endemic to Texas, from the southern part of eastern Texas, westward to the plains region. Shinners notes that *K. cespitosa* often grows with either *K. occidentalis* or *K. gracilis* but intergrades do not seem to occur.

Plants of the annual *Krigia virginica* generally have two flowering forms. Plants in spring have the leaves crowded in a rosette, are almost scapose and largely unbranched. After flowering and fruiting, the plants tend to die back, losing most of the basal leaves, but later begin to grow and flower again, becoming more branched, taller, and often bushy in appearance, with slender, mostly entire leaves (cf. Holm, Shinners).

Chromosome numbers reported for three of the four species of sect. KRIGIA form a polyploid series, $2n = 10$, 20, and 60 (59). Both diploids and tetraploids have been found in *K. biflora* by Chambers, who reported that the tetraploids behave as autoploids and have reduced pollen fertility. *Krigia montana*, a tetraploid, has high pollen fertility. Chambers found near Asheville, N. C., a hexaploid population ($2n = 30$) that may have originated by allopolyploidy from hybrids between diploid *K. biflora*, $2n = 10$, and *K. montana*, $2n = 20$. The hexaploid shows somewhat irregular meiosis but greater pollen fertility than tetraploid *K. biflora*. Morphologically, the hexaploid is most likely to be confused with *K. montana* "which it resembles in the 'key' character of a leafy-bracted inflorescence," although in flower color and some details of the inflorescence and fruit it varies in the direction of *K. biflora*. In crossing attempts involving the two species and the hexaploid, seedlings were obtained from *K. montana* × *K. biflora* ($4x$) and from hexaploid × *K. biflora* ($4x$). No other hybrids, either artificial or natural, seem to have been reported.

In sect. CYMBIA, the chromosome number of *Krigia cespitosa* has been reported as $2n = 8(?)$. Other counts for this species, as well as for the others in the section, are needed before the significance of this number in relation to those found in sect. KRIGIA can be determined.

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though page 57 of *Florula Ludoviciana* had priority over page 149 of the same book (all of which was published at the same time). Other authors, some of whom use the combination *Serinia oppositifolia* (Raf.) Kuntze for this species, have treated the two names in the same way. Page priority, however, is not recognized under the International Code of Botanical Nomenclature. Because of the correction made by Rafinesque on page 149, it is clear that *Krigia oppositifolia* Raf. was "not accepted by the author in the original publication" (ICBN, 1972, Art. 34) and was therefore not validly published. *Serinia cespitosa* Raf. is a validly published name and the basionym for the combination made here. I am grateful to Dr. Carroll Wood for his helpful advice on this nomenclatural problem. — K. L. CHAMBERS, Oregon State University, Corvallis, Oregon 97331.

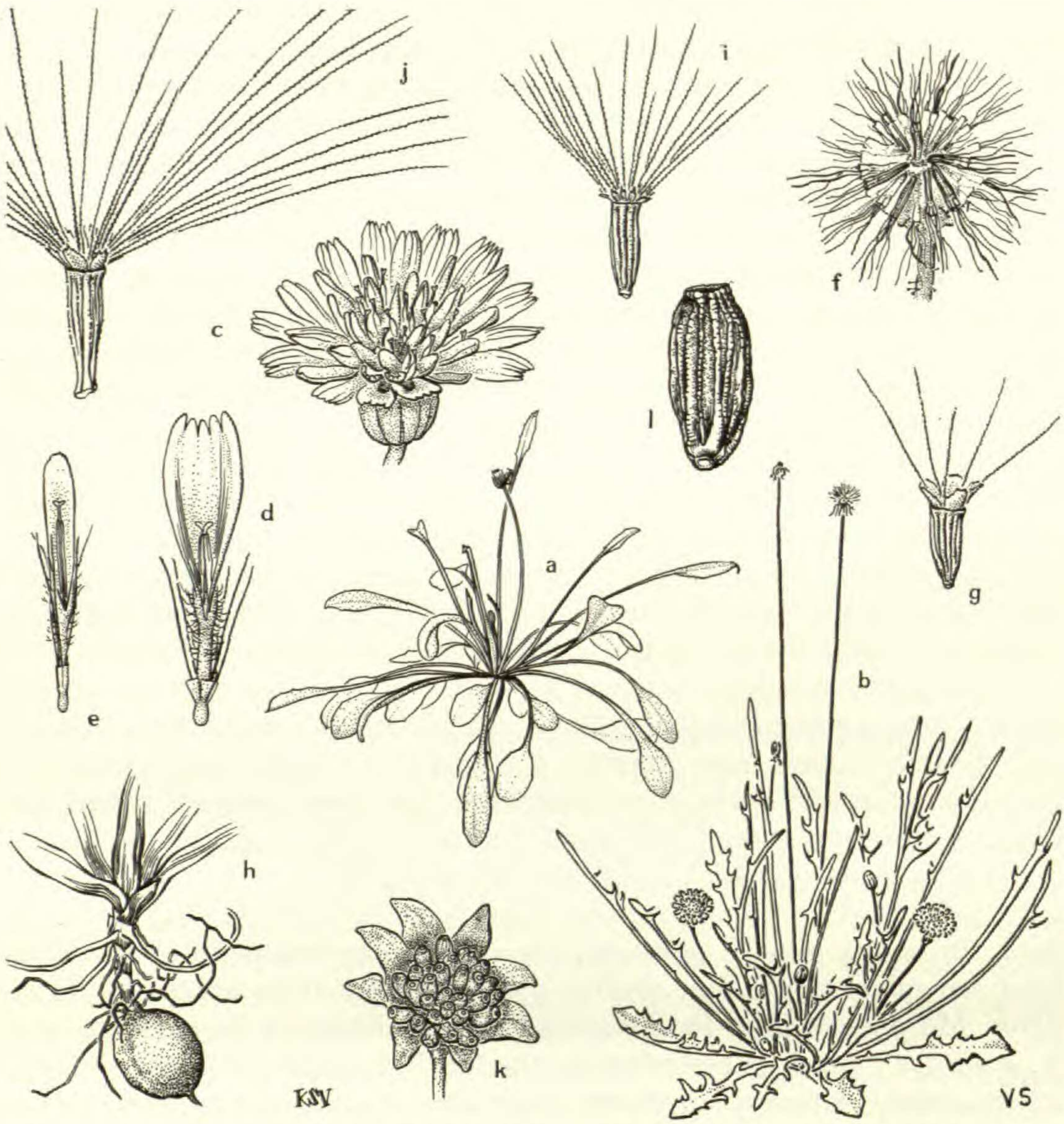

FIGURE 2. **Krigia.** a–g, *K. virginica*: a, plant in early spring phase, flowering about to begin, × 1/2; b, plant in later flowering phase, × 1/2; c, head of flowers, tips of involucral bracts not visible, × 3; d, flower from outer part of head, × 6; e, flower from center of head, × 6; f, head in fruit, only some flowers pollinated, to show spherical arrangement of achenes, the involucral bracts reflexed, not visible, × 3; g, achene — note pappus of five bristles and five scales, × 6. h, i, *K. Dandelion*: h, base of plant showing tuber, × 1; i, achene with pappus of scales and bristles, × 6. j, *K. biflora*: achene, with pappus of scales and long bristles, × 6. k, l, *K. cespitosa*: k, cuplike involucre with mature achenes, × 3; l, achene, × 12.

At least *K. virginica* and *K. cespitosa* seem to be self-compatible, and both set varying numbers of fruit in the absence of pollinators. The heads of flowers expand in the morning in sunlight, close in early afternoon. In both species an individual head opens for about three successive days (obs. C. E. Wood).

The anatomy of *Krigia Dandelion* was investigated by Holm, who found in the root, in addition to the usual articulated laticiferous ducts that occur in root, stem, and leaf, a series of endodermal oil ducts that cor-

respond to those found in some other Lactuceae but contain no oil. These ducts appear to be rare in the Compositae but have been found in *Scorzonera*, *Scolymus*, and *Tragopogon*, all members of the Lactuceae but none related to *Krigia*.

Bentham & Hooker assigned *Krigia* to subtribe Hyoseridinae, placing it in their classification between *Microseris* and *Phalacroseris*, but assigned *Serinia* (as *Apogon*), here included in *Krigia*, to subtribe Lapsaninae, along with *Hispidella* and *Lapsana*. Hoffmann maintained *Krigia* and *Serinia* as separate genera but assigned them to a rather heterogeneous subtribe Cichoriinae, which included 20 genera. In contrast, Stebbins assigned *Krigia* (including *Serinia*) to subtribe Microseridinae, which included *Pyrrhopappus*, to which he thought *Krigia* closely related, and Jeffrey also associated *Krigia* with *Pyrrhopappus*, *Picrosia*, and *Microseris* in the *Microseris*-series of his *Microseris*-subgroup, *Tolpis*-group. However, K. L. Chambers, who is studying the biosystematics of the group, comments that "*Krigia* is a very cohesive genus which is quite isolated taxonomically from the other genera that are placed with it in the subtribe Microseridinae" (Letter, Aug. 1972).

The genus has no economic importance, although several of the annual species are sometimes minor weeds in cultivated ground.

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STANDLEY, P. C. A revision of the cichoriaceous genera *Krigia*, *Cynthia*, and *Cymbia*. Contr. U.S. Natl. Herb. **13:** 351–357. 1911.

3. **Pyrrhopappus** A. P. de Candolle, Prodr. 7: 144. 1838, nom. cons.

Glabrous or pubescent annual or perennial herbs with subscapose or leafy stems arising from a taproot. Heads solitary to several on long pe-

duncles in an open raceme. Involucre campanulate, often with a white tomentum at the base, consisting of two rows of bracts, the outer in the form of a calyculus, the inner long, marginally scarious, abruptly keeled on the abaxial side near the tip (the keel up to 1 mm. high producing the appearance of a bifurcate apex) and becoming elongate and stiffened, spreading and finally reflexed as the achenes mature; receptacle slightly convex, naked. Corolla monochromatic yellow (sometimes dark on the underside of the ligule), rarely cream colored (and then pink streaked beneath). Anthers with small tails. Style branches short, obtuse, flattened. Achenes with a terete to fusiform body with broadly rounded ridges, with a long, slender, brittle beak, the beak often breaking just beneath the persistent pappus; pappus of numerous shining capillary hairs, tawny to purplish tan or orange-tan in color and subtended by a villous ring of minute hairs. (Including *Sitilias* Raf.) TYPE SPECIES: *P. carolinianus* (Walter) DC. (*Leontodon carolinianus* Walter), typus cons. (Name from Greek, *pyrros*, fire colored, and *pappos*, pappus.) — FALSE DANDELION.

A genus of five species (fide D. K. Northington) indigenous to the southern part of the United States and northern Mexico. *Pyrrhopappus carolinianus*, $2n = 12$, and *P. georgianus* Shinners represent the genus in the Southeast, and *P. grandiflorus* (*P. scaposus* DC.), *P. multicaulis* DC. (including *P. Geiseri* Shinners, fide Northington), $2n = 12$, and *P. Rothrockii* Gray, $2n = 12$, occur to the west of our region.

Pyrrhopappus carolinianus, an annual plant, occurs in open woods, fallow fields, roadsides, and prairies from Delaware and southeastern Virginia southward to Florida and west to Illinois, Kansas, Oklahoma, and Texas. The closely related *P. georgianus* has a more limited distribution on the Coastal Plain of South Carolina and Georgia to northern and central Florida. As delimited by Shinners, *P. georgianus* is apparently a perennial plant (the top of the woody tap root often with short branches, each with a rosette of leaves) 12–50 cm. tall, with 0–3 leaves and 1–5 reduced leafy bracts below the inflorescence, and the heads 30–100-flowered, the anthers 4–6 mm. long, and the achene body 5.5–7 mm. long with a beak 7–11 mm. long. *Pyrrhopappus carolinianus*, in contrast, is a mostly taller (15–120 cm.) annual, with 3–12 leaves below the inflorescence (the upper gradually smaller) and the heads 75–165 flowered, the anthers 2–4 mm. long, and the achene body 4–6 cm. long with a beak 7.5–10.5 mm. long.

Northington, who has recently studied the genus in detail, has concluded (letter) on the basis of chemosystematic, cytological, and populational morphological studies plus extensive field observations (data not yet published) that "this genus is an actively speciating group of taxa which are often morphologically very variable but with recognizable species."

Although Bentham & Hooker placed *Pyrrhopappus* in the subtribe Lactucinae D. Don ("Lactuceae") with *Lactuca, Sonchus*, and *Prenanthes*, it seems to belong more naturally with *Krigia* in the Microseridinae, as

suggested by Stebbins. The habit of these two genera is strikingly similar, and both have ovate, obtuse, flattened style branches and orange pollen (except for white-flowered plants of *Pyrrhopappus*). It is also noteworthy that one species of each genus, *K. Dandelion* (L.) Nutt. and *P. grandiflorus* Nutt., produces a small underground tuber. Jeffrey has also allied *Pyrrhopappus* with *Krigia, Serinia* (= *Krigia*), *Microseris*, and *Picrosia*, these genera constituting his *Microseris*-series, of the *Microseris*-subgroup of the *Tolpis*-group in the Lactuceae.

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Subtribe **Stephanomeriinae** Stebbins in Solbrig, Taxon **12**: 235. 1963.

4. **Lygodesmia** D. Don, Edinburgh New Philos. Jour. **6**: 311. 1829.

Glabrous perennial herbs with stiff, branching stems. Basal leaves linear, entire [or pinnatifid] or absent; stem leaves usually reduced to narrow bracts or small scales. Heads solitary, terminating the ultimate branches; involucre cylindrical or cylindroid, composed of 5(–9) subequal lanceolate interior bracts with scarious margins and more numerous very short exterior bracts; receptacle flat, naked. Corolla ligulate, 5-dentate at apex, pink or rose-colored to pale violet or purple (rarely white), never yellow. Anthers sagittate at base or with sharp auriculate or acuminate basal appendages; pollen echinolophate. Style branches slender and elongate. Achenes subterete, smooth on the abaxial surface, longitudinally ribbed on the adaxial surface, truncate at apex; pappus of numerous pale tan-colored capillary bristles. LECTOTYPE SPECIES: *L. juncea* (Pursh) Hooker; [5] see Britton & Brown, Illus. Fl. No. U.S. ed. 2. **3**: 322. 1913. (Name from Greek, *lygos*, twig, and *desme*, bundle, in reference to the cluster of sticklike stems.) — SKELETON WEED, FLOWERING STRAW, RUSH-PINK.

[5] This combination traditionally has been attributed to David Don, the name cited as *Lygodesmia juncea* (Pursh) D. Don, but Don merely listed the species that he thought belonged to his new genus without making formal transfers. The combination was first made by Hooker in Fl. Boreali-Am. **1**: 295. 1834.

A well-defined genus of eight species, mostly of western North America, primarily in dry areas, prairie lands, and on the Plains. One species, isolated from its congeners, is restricted to our area, another enters it locally in Arkansas.

Lygodesmia aphylla (Nutt.) DC., rose-rush, rushweed, a distinctive species of the acid, sandy soils of open pinelands on the Coastal Plain of southern Georgia and Florida, is a sparsely branched plant from a slender, deep-seated rootstock. The stiffly ascending stems appear to be leafless since the stem leaves are reduced to small brown scales. The few very narrow, linear, entire basal leaves often have withered by the time flowering occurs. The involucre is usually 15–20 mm. tall, the heads are relatively large (3–5 cm. across when the corollas are expanded) with about 10 rose-pink to lavender (rarely white) flowers, and the achene is 10–15 mm. long. Its closest relative (fide Tomb) is *L. texana* (Torrey & Gray) Greene (*L. aphylla* var. *texana* Torrey & Gray), $2n = 18$, which occurs in rocky, calcareous soils in Oklahoma, Texas, New Mexico, Coahuila, and Chihuahua. The flowering heads are approximately the same size as those of *L. aphylla*, but the basal leaves and lower stem leaves, while almost linear, are wider and are pinnatifid, with short linear lobes.

The lower and much more branched *Lygodesmia juncea*, skeleton weed, in which all of the leaves are linear-subulate and bractlike, is widely distributed in dry areas, from British Colombia and Alberta to Manitoba and Minnesota, southward to northwestern Missouri, Oklahoma, Texas, New Mexico, and Nevada. It occurs locally in our area only in the region of Little Rock, Arkansas (fide Tomb). The involucre of this plant is usually 10–15 mm. high, the heads usually have five pink to pale violet (or rarely white) florets, and the achene is 6–10 mm. long. The plant has long been suspected of being poisonous to cattle, and Kingsbury lists it among 47 weedy species in which toxic concentrations of nitrates have been measured.

The reduction of leaf surface in most species presumably is an adaptation to the xeric or exposed habitats occupied by the members of the genus.

Stebbins allied *Lygodesmia* with ten genera (all North American except *Thamnoseris* Philippi, an endemic of San Felix and San Ambrosio islands off the coast of Chile) in the subtribe Stephanomeriinae, noting that *Stephanomeria, Lygodesmia, Chaetadelpha, Rafinesquia,* and *Thamnoseris* constitute one of two groups of genera within the subtribe. Jeffrey indicated similar relationships but removed *Thamnoseris* to a completely different alliance. Among these genera *Lygodesmia* apparently is distinctive in its unusually elongate style branches and echinolophate pollen. It appears to be most closely related to *Stephanomeria,* which was united with it by Shinners, who thought that the single distinguishing character (a capillary pappus in *Lygodesmia,* a plumose one in *Stephanomeria*) was not sufficient for maintaining them as separate genera. Stebbins maintained, however, that the two are "no closer to each other

in the sum total of their habital and floral characteristics than are many other pairs of generally recognized genera of the Cichorieae [Lactuceae]. In addition to the pappus, differences exist between most species of the two genera with respect to the character of the pollen grains, the length of the style branches, and the size and shape of the achenes." Tomb (1970b) has recently followed the same course, noting that *Lygodesmia* and *Stephanomeria* differ in base chromosome numbers ($x = 9$ *vs.* 8), pollen grains (echinolophate *vs.* echinate), achenes, and cotyledon morphology.

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Subtribe **Scorzonerinae** Dumortier, Fl. Belg. Prodr. 1827, "Scorzonereae."

5. **Tragopogon** Linnaeus, Sp. Pl. 2: 789. 1753; Gen. Pl. ed. 5. 346. 1754.

Coarse biennial or perennial caulescent herbs with alternate, linear-lanceolate, leaves. Heads solitary at the ends of long stiff, erect peduncles. Involucre of one series of stiff, lanceolate bracts; receptacle flat or slightly convex, foveolate, with small scarious rims around the foveolae. Corolla purple or yellow, usually conspicuous, but sometimes hidden within the capitulum. Anthers sagittate or auriculate at base. Style branches thin, terete. Achenes slender, 5–10-ribbed, long beaked (sometimes the outer series short beaked), the surafce rugose or muricate [hispid]; pappus of numerous plumose bristles borne on a disc, the outer series sometimes expanded at the base. LECTOTYPE SPECIES: *T. pratensis* L.; see Britton & Brown, Illus. Fl. No. U.S. ed. 2. 3: 313. 1913. (Name from Greek *tragos*, goat, and *pogon*, beard, referring to the appearance of the pappus.) — GOAT'S BEARD.

A genus of 40–50 species indigenous to Europe, Africa, and temperate Asia. Three species are widely naturalized in North America. The three are quite distinct in their morphology, differing in habit; color, shape, crisping and curling of the leaves; color, number and shape of the involucral bracts; number of flowers in a head; relative lengths of the involucral bracts and corolla limb (ligule); shape and relative length of the beak and body of the fruit; and color of the fruit and pappus (Ownbey).

Tragopogon porrifolius L., salsify, oyster plant, $2n = 12$, characterized by pale to deep violet corollas shorter than the bracts (these usually 8), strongly inflated peduncles, and a brownish pappus, is widely escaped from cultivation and is naturalized from Maine to the Pacific coast, south to New Mexico and Georgia. *Tragopogon pratensis* L., $2n = 24$, has chrome-yellow corollas, those of the outer ones equalling the 8(–13) involucral bracts, leaves with crisped margins and recurved tips, peduncles that are scarcely inflated even in fruit, and a whitish pappus. It has been recorded as far west as Idaho and southward to Tennessee and Arizona. *Tragopogon dubius* Scop. (including *T. major* Jacq.), $2n = 12$, with pale lemon-yellow corollas all shorter than the bracts, strongly inflated peduncles, usually 13 bracts and over 100 flowers in each head, and a whitish pappus, occurs transcontinentally and extends southward to North Carolina, Tennessee, and New Mexico.

Natural hybrids between all three species have been found in both Europe and North America. The first recorded artificial hybrid was produced by Linnaeus between *T. pratensis* and *T. porrifolius*. Ownbey has demonstrated that two new species of *Tragopogon* have arisen by hybridization followed by doubling of the chromosome number and has provided not only the best-documented examples of this type of speciation within recent time, but has found evidence for polytopic origin of at least one species. The F_1 diploid hybrids are frequently encountered but are usually highly sterile; the morphology of the hybrids differs depending upon

which species is the carpellate parent. Doubling of the chromosome number simultaneously restores fertility and isolates the amphiploid reproductively from its diploid parents. *Tragopogon miscellus* Ownbey, $2n = 24$, the amphiploid (amphidiploid, allotetraploid) of *T. dubius* × *T. pratensis*, was described from two colonies about a mile apart near Moscow, Idaho; and *T. mirus* Ownbey, $2n = 24$, the amphiploid of *T. dubius* × *T. porrifolius*, was described from a colony in Pullman, Washington, and one at Palouse, about 15 miles away, the two apparently having originated independently. Both amphiploids are easily recognized by their "gigas" features. They "differ in none of their characters from the corresponding diploid hybrids, but they are much larger in every way. The stems and leaves are thicker, coarser, more massive and succulent. The heads are larger both in flower and in fruit, and the fruits larger and thicker. The mean volume of the spherical pollen grains is almost precisely the sum of the mean volumes of those of the parental species. The fertility averages between 52 and 66 per cent, although there is wide variation in individual plants beyond these limits. In all four colonies, the amphiploids occurred with both the parental species, and the diploid F_1 hybrid. In one patch, three species, three F_1 hybrids and one amphiploid species grew together" (Ownbey, 1950, p. 493). Recent studies of the flavonoid chemistry have further confirmed the amphiploid origin of both new species (Brehm & Ownbey). Brown & Schaack have recently found *T. miscellus* and *T. mirus* growing with the three parental species at Flagstaff, Coconino County, Arizona. These occurrences presumably represent further examples of the polytopic origin of the two amphiploid species.

The effects of light on germination of the dimorphic achenes of *Tragopogon dubius* and *T. porrifolius* have been investigated by Heilpern, who found that the outer, strongly curved, darker colored achenes germinate much faster in light, and slightly faster in darkness, than the inner, straight, paler achenes. Allard found that *T. dubius* seems to require long days for good growth and the initiation of flowering. Optimum reproduction occurs between 40° and 50° N. latitude, and Allard concluded that the southern distributional limit of the species would coincide with the latitude at which the day length is always too short to allow flowering.

In addition to the amphiploids, thirteen diploid species in the genus have been investigated cytologically. In eleven $2n = 12$, in one $2n = 12$ or 14, and in one $2n = 14$.

The cultivated salsify, *Tragopogon porrifolius*, is also called oyster plant because its carrot-shaped taproot (prepared in numerous ways like potato) is said to have a taste similar to that of oysters. In Europe, the shoots are sometimes eaten like asparagus, the leaves as salad greens, and the root is occasionally dried and ground as a substitute for chicory for blending with coffee. Extracts from the roots are used locally as a diuretic.

Both Stebbins and Jeffrey are in agreement that *Tragopogon* is allied to *Scorzonera* and *Tourneuxia*, but Stebbins treats the three as constituting a subtribe, Scorzonerinae, while in Jeffrey's classification they comprise the *Scorzonera*-subgroup of his *Hypochoeris*-group.

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Subtribe **Hypochoeridinae** Lessing, Synopsis 130. 1832, "Hypochoerideae."
(Leontodontinae C. H. Schultz Bipontinus, 1850.)

6. **Hypochoeris** Linnaeus, Sp. Pl. **2**: 810. 1753, "Hypochaeris"; Gen. Pl. ed. 5. 352. 1754.[6]

Annual or perennial herbs with scapose or paniculate flowering stems. Leaves basal, sometimes also alternate up the stem, oblanceolate in outline, entire or toothed [pinnatifid]. Involucre composed of several series of imbricate bracts with scarious margins and increasing in size toward the inside, the outer surface glabrous, lanate, or strigose; receptacle flat, with a scarious scale subtending each floret; both bracts and scales enlarging in fruit. Corolla yellow [white, or orange], sometimes with a tuft of hairs at the outside of the throat. Anthers sagittate at base. Style with a glandular base and thin, terete branches. Achenes glabrous, 10-ribbed

[6] In *Species Plantarum* Linnaeus used the spelling *Hypochaeris*, but in *Genera Plantarum*, ed. 5, he used *Hypochoeris*. In the preponderance of his later work he used the spelling with *ae*, rather than *oe* (as did his contemporaries), but he was inconsistent. In accordance with regulation 2 of Article 74 of the International Code of Botanical Nomenclature, 1972, the spelling with *oe*, which is more correct philologically, is used here. Most recent authors have also used this spelling.

and upwardly scabrous on the ribs, either monomorphic and beaked, or dimorphic, with the outermost achenes beakless, the inner ones beaked; pappus in one or two series, setose and/or plumose, white or tawny. LECTOTYPE SPECIES: *H. glabra* L.; see Bentham & Hooker, Gen. Pl. 2: 520. 1873, who treated this species as the only member of sect. EUPHYPOCHOERIS; see also Britton & Brown, Illus. Fl. No. U.S. ed. 2. 3: 309. 1913. (Name from Greek *hypochoiris*, used by Dioscorides for some plant, and also mentioned by Pliny as *hypochoeris*, the name perhaps derived from *hypo*, for, and *choiros*, pig, these animals being fond of its roots.) — CAT'S EARS.

A genus containing about 50 (Stebbins, *et al.*) to 100 (Cabrera) species in five or six sections (Hoffmann; Stebbins, *et al.*) with an unusual pattern of distribution. Most of the species are indigenous to extra-tropical South America, but about ten are European, and one is indigenous to Asia. Two European and two South American species are naturalized in North America; all four occur in the southeastern United States.

Both naturalized species of sect. HYPOCHOERIS, characterized by a pappus of an outer series of short bristles and an inner of much longer plumose ones, occur in the Southeast. *Hypochoeris glabra*, $2n = 10$, an annual, has been collected in scattered localities in the northeastern United States and is more extensively naturalized southward to Florida and Alabama, as well as in western North America from British Columbia to California. The perennial *Hypochoeris radicata* L., $2n = 8$, is widely naturalized from Newfoundland to Ontario, south to Missouri, Louisiana, Alabama, Georgia, and South Carolina, and from California to British Columbia. The two are easily distinguished by the uniformly beaked achenes of *H. radicata* versus the dimorphic ones of *H. glabra*. In the latter the outermost achenes are truncate (beakless) and have a pappus composed of short barbellate outer bristles and an inner series of much longer ones that are densely plumose in the lower third and remotely plumose and barbellate above, while all of the inner achenes are long beaked and with a pappus of shorter outer setose and barbellate series and an inner plumose and barbellate one. Almost completely sterile hybrids between the two species have been reported from Europe, but the cytology of these does not seem to have been investigated.

Section ACHYROPHORUS DC. in Lam. & DC., in which the pappus is composed entirely of plumose bristles, is represented in our area by the South American *Hypochoeris Tweedii* Hooker & Arn. (*H. brasiliensis* (Less.) Griseb. var. *Tweedii* (Hooker & Arn.) Baker), $2n = 8$, and by *H. microcephala* (Schultz Bip.) Cabrera var. *albiflora* (O. Kuntze) Cabrera, $2n = 8$, which is spreading rapidly in southeastern Texas (fide Tomb) and has been collected at Lake Charles in southwestern Louisiana (Thieret). *Hypochoeris Tweedii*, indigenous to Uruguay and northeastern Argentina but now distributed in disturbed habitats primarily on the Coastal Plain from North Carolina to Florida and Alabama, has been reported as both *H. brasiliensis*, with which it is perhaps conspecific (al-

though it is maintained as a distinct species by Cabrera), and *H. elata* (Wedd.) Griseb., a plant of the Andes at altitudes above 3500 meters. The campanulate involucre of *H. Tweedii*, 12–15 mm. tall by 6–8 mm. in diameter at anthesis with the exterior bracts linear, obtuse, and hispid, is characteristic. The involucre of *H. brasiliensis* differs in its linear, slightly obtuse and lightly lanuginose, exterior bracts. *Hypochoeris microcephala* var. *albiflora*, indigenous to Brazil, Uruguay, and northeastern Argentina, has white flowers and a narrowly cylindric involucre 10 mm. tall by 3–4 mm. in diameter at anthesis, with the outer bracts either glabrous or laxly lanuginose (Cabrera).

The flowers of *Hypochoeris radicata* are visited by a variety of insects, including bees, butterflies, flies, and small beetles, but can also be self-pollinated in at least three ways (Hagerup). The diurnal opening and closing of the head in response to light brings stigmas into contact with pollen on adjacent flowers; or self-pollination can occur through the agency of rain, the corollas of this species having on the outside of the throat a tuft of hairs that with those of the other flowers prevents water from penetrating between the flowers and traps water on the open head in a sort of pool on which the pollen can float into contact with the stigmas; or pollen can be carried from one flower to another by the movements of tiny insects of the genus *Thrips* that live in the flower heads, eating pollen and nectar and laying their eggs on the tips of the receptacular scales.

Diploid chromosome numbers reported for the genus are 6, 8, 10, 12, and 16. Stebbins has postulated that the base number of the Old World species, which he considers to be the most primitive, is five, but the wide variation in the genus is perhaps indicative that more than one base number is involved.

Hypochoeris is evidently related to *Leontodon* (q.v.) from which it differs conspicuously in the presence of bractlike receptacular scales. It is odd that both genera have species with dimorphic achenes.

The achenes of some European species are dried and extracted like those of *Arnica* for medicinal use (Fournier). The leaves are also eaten as a salad or cooked greens similar to those of *Taraxacum*, and Hooker & Arnott noted in the original description of *Hypochoeris Tweedii* that in Buenos Aires ". . . it is frequently employed as Endive."

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7. **Leontodon** Linnaeus, Sp. Pl. **2**: 798. 1753; Gen. Pl. ed. 5. 349. 1754, nom. cons.

Perennial [or annual] scapose [or subscapose] herbs with simple [or sparingly branched] flowering stems. Basal rosette of lanceolate to lyrate, dentate, parted [or entire] leaves with forked or simple hairs [or glabrous]. Heads solitary, terminating naked scapes [or scapes bracteate, sparingly branched, each branch with a solitary head]. Involucre of an inner series of slightly imbricate lanceolate glabrous or pubescent bracts and an outer series of much shorter bracts; receptacle flat, naked, pitted, the pits often with toothed or ciliate margins. Corolla yellow. Anthers with sagittate, auriculate, or setose basal appendages; pollen spherical, spiny. Style branches thin, terete. Achenes ± cylindrical, the outermost truncate, beakless with a cuplike pappus of short scarious scales, the inner beakless or short beaked with a pappus of 2 rows of bristles, the inner plumose with dilated bases, the outer much shorter, simple and scabrid [or achenes all similar, beaked or beakless, with a pappus of two rows of hairs (plumose and simple) or with only a single row of plumose hairs dilated at base]. (*Virea* Adanson.) LECTOTYPE SPECIES: *L. hispidus* L., typus cons. (Name from Greek, *leon*, lion, and *odous, odontos*, tooth, from the coarsely toothed leaves.) — HAWKBIT.

A genus of 40 or fewer species in eight or nine sections native to Europe, Asia, northern Africa, and the Azores; three species adventive in North America, one of these sporadic in the southeastern United States.

The European *Leontodon taraxacoides* (Vill.) Mérat (*L. nudicaulis* auct., *L. nudicaulis* subsp. *taraxacoides* (Vill.) Schinz & Thell., *L. Leysseri* (Wallr.) G. Beck, *L. nudicaulis* f. *Leysseri* (Wallr.) Ascherson & Graebner), $2n$ = 8, of sect. THRINCIA (Roth) Dumort., characterized by dimorphic achenes, the outermost beakless and curved, with a cuplike crown of short scales, the inner more or less beaked with a pappus of long plumose hairs and of shorter scabrid bristles, has been collected in our region in at least North Carolina and Alabama. It is of more frequent

occurrence in the Northeast (Massachusetts, Rhode Island, Connecticut, and New York) and has also been found in at least Pennsylvania, the District of Columbia, Illinois, and Texas, and from California northward to British Columbia, mostly near the coast. Its perennial habit (from a short, erect rootstock), leaves (at least beneath) with multicellular hairs bifurcate at the tip, bractless unbranched scapes, yellow flowers (the outermost gray-violet beneath), and dimorphic achenes are characteristic.

Leontodon autumnalis L., $2n = 12, 24$, of sect. OPORINIA (D. Don) W. D. Koch (all achenes similar, with a pappus of a single whorl of plumose hairs dilated at the base, and leaves with simple unforked hairs or glabrous), is widely naturalized to the north of our area in disturbed soils in Atlantic North America from Greenland and Newfoundland, south to Pennsylvania, and sporadically inland to Michigan, and in western North America from California to British Columbia. The pappus and the scaly-bracteate scapes are characteristic. *Leontodon hispidus* L. var. *glabratus* (W. D. Koch) Bischoff (*L. hastilis* L.), $2n = 14$, of sect. LEONTODON (all achenes similar, with a pappus of outer short, simple, scabrid bristles and inner, much longer plumose ones, and leaves [when pubescent] with hairs bifurcate at the tip), has been collected locally in Connecticut. Most of the range given for this plant and for *L. hastilis* var. *vulgaris* W. D. Koch (*L. hispidus* var. *hispidus*) in current manuals is based on misidentified specimens of *L. taraxacoides*. The rather large heads on ebracteate, unbranched scapes and the monomorphic achenes with a double pappus are characteristic. Only the glabrous form seems to be adventive in North America.

Chromosome numbers of $2n = 8, 10, 12, 14$, and 24 have been reported for species of *Leontodon*. Hybrids between various European taxa have been reported, but only that between *L. taraxacoides* (*L. Leysseri*), $2n = 8$, and *L. hispidus*, $2n = 14$, appears to have been studied cytologically. Six of the chromosomes of both parental taxa bear satellites, and four of the six have subterminal centromeres, while the remaining two have median centromeres. The hybrid ($2n = 11$) has, however, only four satellited chromosomes, all with subterminal centromeres, the two with median centromeres apparently having lost their satellites (Elliot).

Bergman found that in *Leontodon hispidus* the Polygonum-type embryo sac occurred in half of the ovaries examined, while the others had the Adoxa-type. He also found that somatic apospory occurred in some florets, and a statistical analysis of its occurrence indicated that it is a recessive genetically controlled character.

Studies by H. Becker (reported in Hegi) showed a difference in germination behavior between the inner and outer achenes of *Leontodon taraxacoides*. The inner ones will germinate in either light or dark, but the circumferential ones will germinate only if exposed to light.

Leontodon has been confused nomenclaturally with *Taraxacum* Wiggers, nom. cons., and *Leontodon Taraxacum* L., the lectotype effectively chosen by Adanson (1763), who removed all other species to a new genus, *Virea*, is *Taraxacum officinale* Wiggers, the type of the name *Taraxacum*.

Leontodon consequently has been conserved (provisionally; cf. ICBN. 1972) with a different type, *L. hispidus*, as suggested by Hitchcock & Green, to avoid the necessity of taking up *Virea* for all the species now known as *Leontodon*. (See Vuilleumier for discussion.)

Bentham (1873) suggested that *Leontodon* is related to *Taraxacum* and to *Hypochoeris*, but in Bentham & Hooker (1873) only the relationship to the latter is noted, although *Taraxacum* is placed in the same subtribe (Hypochoeridinae) with the two. Stebbins placed *Leontodon* in the subtribe Leontodontinae (= Hypochoeridinae) and *Taraxacum* in the Crepidinae, and Jeffrey suggested similar affinities for the two genera.

The genus has no economic importance, except for a few species that are lawn weeds in some areas.

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8. **Picris** Linnaeus, Sp. Pl. **2**: 792. 1753; Gen. Pl. ed. 5. 347. 1754.

Branched, perennial, hispid herbs with oblanceolate to spathulate basal (sometimes called cauline) leaves with entire, sinuate-dentate [or pinnately parted margins]. Heads long-pedunculate, arranged in a corymbose, determinate inflorescence. Involucre often swollen at base (especially after anthesis), composed of inner, imbricate, lanceolate bracts and several outer series progressively decreasing in size [or with a sharply dis-

tinct outer series of relatively large foliaceous bracts]; receptacle flat, naked or fimbrillate. Corolla yellow. Anthers with sagittate bases of acute auricles. Style branches thin. Achenes subterete or angled, frequently curved, 5–10-ribbed, all similar [or outermost distinct in some species], constricted at apex [or beaked], horizontally rugose, glabrous; pappus plumose, deciduous [with the beak]. LECTOTYPE SPECIES: *P. hieracioides* L.; typified by the removal of two of the four original species to *Helminthia* Juss. and of the third to *Hieracium*. (Name from Greek, *picros*, bitter, in reference to the taste of the plant). — OX-TONGUE, BITTER-WEED.

A genus of perhaps 35 (probably fewer) species indigenous to the Old World and assigned (on the basis of characters of the involucral bracts and achenes) to four sections (Hoffmann). *Picris hieracioides*, $2n = 10$, of sect. PICRIS, and *P. echioides* L., $2n = 10$, of sect. HELMINTHIA (Juss.) Hoffm., are adventive in northeastern North America, but only the former has been reported from our area, where it occurs in western North Carolina (cf. Ahles *et al.*). *Picris hieracioides* has leaves with stiff, pointed hairs and some hairs that are bifurcate at the tip with the divisions recurved, stems with similar bifurcate hairs, and the involucral bracts (the outer progressively smaller) pubescent and with bifurcate hairs. The achenes are beakless, and the pappus is deciduous. In *P. echioides* the pubescence includes hairs that are 3- or 4-furcate at the tip, with the divisions recurved in the manner of a grappling hook; the outermost involucral bracts are large and spiny; and the achenes are slender beaked. It has been recorded from scattered localities from eastern Canada south to the latitude of the District of Columbia.

Chromosome numbers of $2n = 10$ have been reported in all nine of the species of *Picris* that have been investigated, but *P. Sprengeriana* Poiret has been reported as having both $2n = 10$ and $2n = 8$. Bergman noted the occurrence of a few rare cases of ameiotic apospory that led to sterile embryo sacs in *P. hieracioides*.

Stebbins assigned *Picris* to subtribe Leontodontinae (properly Hypochoeridinae when used in his sense), along with *Hypochoeris*, *Leontodon*, *Urospermum*, *Hedypnois*, *Garhadiolus*, and *Rhagadiolus*; and Jeffrey retained the same alignment of genera in the *Hypochoeris*-series, of his *Hypochoeris*-subgroup, *Hypochoeris*-group.

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Subtribe **Crepidinae** Dumortier, Fl. Belg. Prodr. 74. 1827, "Crepideae."

9. **Sonchus** Linnaeus, Sp. Pl. 2: 793. 1753; Gen. Pl. ed. 5. 347. 1754.

Robust annual or perennial herbs with caulescent, branching, striate, often pubescent flowering stems arising from a taproot or creeping rhizome. Basal leaves absent or in a rosette; if present, lanceolate, spathulate, runcinate, or lyrate, serrate, dentate, or parted. Stem leaves similar, becoming more lanceolate and smaller up the stem, clasping, with acute or rounded auricles. Inflorescence a panicle of few to numerous heads. Involucre of several series of bracts; the inner lanceolate, subequal, slightly imbricate, sometimes marginally scarious, glabrous or pubescent; the outer much smaller, ovate; receptacle flat or concave, naked, becoming convex when the achenes are shed. Corolla yellow. Anthers sagittate at the base; pollen spherical, tricolporate, the surface with 15–20 lacunae surrounded by ridges surmounted by elaborate spines. Style branches thin, terete. Achenes monomorphic [dimorphic in some], flattened, narrowed at both ends, striated, sometimes rugose; pappus capillary, often composed of hairs and bristles (sensu Boulos), abundant, soft, white. LECTOTYPE SPECIES: *S. oleraceus* L.; see Britton & Brown, Illus. Fl. No. U.S. ed. 2. 3: 306. 1913. (Name from Greek, *sonchos*, a name used by Dioscorides, Theophrastes, and Pliny for a prickly plant.) — SOW-THISTLE.

A genus of some 70 species in three subgenera (Boulos) and indigenous to Europe, Asia, and northern Africa. The most primitive subgenus, ORIGOSONCHUS Boulos, found in tropical West Africa, is comprised of perennial species with few-headed inflorescences. Subgenus DENDROSONCHUS Webb ex Schultz Bip. is composed of a group of shrubby species with umbellate or cymose arrangements of heads. The woody habit of this subgenus is correlated with its adaptation to island life (see Carlquist, 1965, Chapter 8). Although a few of its species occur on the African mainland, the majority are restricted to Madeira and the Canary and Cape Verde islands. The most advanced subgenus, SONCHUS, is possibly derived from members of subg. DENDROSONCHUS (cf. Boulos), although many species have become annuals. The morphology of the species of subg. SONCHUS is variable, and numerous species, three of which are naturalized in the southeastern United States, have become cosmopolitan weeds.

Sonchus oleraceus L., sow-thistle, $2n = 16, 32$, is easily recognized by its annual habit (taproot), pinnately parted lyrate leaves with an arrow-shaped terminal segment, stem leaves with pointed auricles, and rugose achenes. This weedy plant now occurs across southern Canada, throughout the United States and in Mexico, the West Indies, and extratropical South America, as well as Australia.

Also naturalized all across the United States and southern Canada, in the West Indies, and in parts of South America, *Sonchus asper* (L.) Hill, $2n = 18$, is distinguished from the preceding species by its perennial habit, stiff, prickly leaves (more dentate than parted), round stem-leaf auricles, and smooth achenes. The third adventive species, the perennial sow-thistle, *S. arvensis* L. (including *S. arvensis* var. *glabrescens* Guenth.,

Grab. & Wimm. and *S. uliginosus* Bieb.), $2n = 18, 36, 45, 54$, and 64, is primarily a species of the northeastern United States and adjacent Canada, but has now been reported in North Carolina. This is actually a polyploid complex involving *S. arvensis*, $2n = 54$ and *S. uliginosus*, $2n = 36$. Boulos considers all of the morphological and chromosomal forms of this complex to belong to one biological species. There are innumerable intermediate specimens resulting from back-crossing, and there is a complete range of chromosome numbers from $2n = 36$ to 64 that would be impossible to assign to a given segregate taxon if it were recognized.

Natural hybridization, apparently without backcrossing and introgression, was reported between *Sonchus oleraceus* and *S. asper* by Barber. Recently, however, Hsieh *et al.* made all possible crosses between *S. oleraceus* ($2n = 36$), *S. arvensis* ($2n = 36$), and *S. asper* ($2n = 18$). Crosses between *S. arvensis* and *S. asper* produced pollen-sterile hybrids that had only partial meiotic pairing in the microsporocytes. The F_1 hybrids resulting from crosses between *S. oleraceus* and either *S. arvensis* or *S. asper* were also pollen-sterile, but, in addition, showed no pairing between parental chromosome complements during meiosis. During normal meiosis of the tetraploid *S. arvensis* and the diploid *S. asper*, bivalents were uniformly formed. In contrast, meiotic cells of the tetraploid *S. oleraceus* normally exhibited both bivalent and tetravalent pairing. Hsieh *et al.*, in contrast to Stebbins *et al.*, concluded that *S. arvensis* is an amphiploid with one chromosome complement from *S. asper* and that the race of *S. oleraceus* studied is an autotetraploid.

Although Bentham considered *Sonchus* closely related to *Lactuca* L., Babcock *et al.*, Stebbins, and Boulos all thought that it must be most closely allied to, and perhaps derived from, *Launaea* Cass., a genus of tropical Africa, Asia, and America. Recent pollen studies by Saad have reinforced this idea and have tended to confirm the subgeneric groupings outlined by Boulos. Jeffrey, in contrast, separates *Sonchus*, *Dendroseris* (sensu lato), and *Thamnoseris* as the *Sonchus*-group (subtribe?), while *Launaea*, *Aethiorrhiza*, and *Reichardia* constitute the *Launaea*-series, *Crepis*-subgroup, *Cichorium*-group.

Chromosome studies of other species in the genus have yielded numbers of $2n = 14, 16, 32, 36, 45, 54$, and 64.

The genus has no particular economic importance except as an annoying weed. In Eurasia *Sonchus* has been used locally as a medicinal plant, the juice being drunk to counteract asthma and stomach ulcers, and applied externally for the relief of earaches. In Asia proper, the sweetened juice of some species is considered to have a laxative effect (cf. Fournier).

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10. **Launaea** Cassini, Dict. Sci. Nat. **15:** 321. 1822.

Perennial [annual], glabrous herbs with a basal rosette and alternate, smaller stem leaves. Leaves pandurate [obovate to lanceolate], coarsely toothed [serrate to more or less entire]. Inflorescence a panicle of numerous [few] heads. Involucre composed of a few series of unequal, scarious [broadly scarious], lanceolate [ovate] bracts; receptacle flat, naked. Florets perfect. Corolla pale yellow. Anthers sagittate at the base. Style branches thin, short. Achenes dimorphic [monomorphic, polymorphic], the outer slightly flattened, with equal muricate ribs; the inner terete, glabrous, lightly but equally ribbed [if monomorphic, all slightly muricate, if polymorphic, gradually changing from one type to the other], beakless [or with a very short, stout beak]; pappus capillary, composed of thin, straight bristles and finer, downy, almost woolly hairs [only straight bristles with or without an outer ring of very short ones], copious, white. (Including *Brachyramphus* DC. and *Microrhynchus* Less.) TYPE SPECIES: *L. bellidifolia* Cass. (Named after French author Jean Claude Mien Mordant de Launay, d. 1816, librarian of the Jardin des Plantes, Paris, and a founder of *Herbier Générale de l'Amateur*, known for his popular writings on gardening and amateur botany.)

A genus of about 30 species in five sections (fide Hoffmann) distributed in Africa, Europe, Asia, southern North America, and the West Indies. Unfortunately, there has not been any modern published revision of *Launaea*, and the generic boundaries between it, *Lactuca*, and *Sonchus* remain obscure. This uncertainty of generic limits has caused our species, *Launaea intybacea* (Jacq.) Beauverd to be placed variously in *Lactuca*

(*L. intybacea* Jacq.), by Bentham & Hooker, by Adams in the *Flora of West Tropical Africa* (1963) and by Long & Lakela; in *Launaea*, by Hoffmann, by Jeffrey, and by Adams in *The Flowering Plants of Jamaica*; or in the segregate genus *Brachyrhamphus* (*B. intybaceus* (Jacq.) DC.), by De Candolle and Small. This species is native to the West Indies, but is now found in rocky areas and waste places in Mexico, northern South America, Florida, the Greater and Lesser Antilles, and subtropical Africa and India. It is the only species of *Launaea* indigenous to the New World. Despite a seemingly erratic geographical distribution, there is no doubt that *L. intybacea* is distinct from both the North American species of *Lactuca* (sect. MULGEDIUM) and the Old World species. It is easily recognized by the basal rosette of large yellow-green leaves and the much-branched inflorescence with pale-yellow-flowered heads.

Most of the species of *Lactuca* have beaked achenes, and all members have a monomorphic pappus and achenes. All members of *Launaea* have beakless achenes that are dimorphic or polymorphic (cf Boulos) and a dimorphic pappus. The presence of soft, white, down-like hairs among the straighter setae of the pappus and the difference between the outer and inner achenes readily distinguishes *L. intybacea* from all of our species of *Lactuca* and *Sonchus*. However, many species of *Sonchus*, like those of *Launaea* have dimorphic achenes and pappus, but the achenes of *Sonchus* are not so markedly dimorphic as those of *Launaea*. The most significant difference between these two genera, in Boulos's opinion, is the amount of fertility displayed by the achenial types within a capitulum. In species of *Sonchus*, all achenes are fertile but in *Launaea*, only one morphological type is fertile. Boulos, however, did not give any criterion for his assertion that achenes were fertile or nonfertile.

Babcock & Stebbins, Stebbins, and Boulos have all postulated that *Sonchus* was derived either from *Launaea* or from *Launaea*-like ancestors. This hypothesis is based on the observation that many features of *Launaea*, such as columnar achenes and the involucral bracts of varying sizes, are found in the most primitive species of *Sonchus*. Jeffrey, however, postulates quite different relationships (cf. *Sonchus*).

Although the chromosome number of *Launaea intybacea* has not been determined, numbers of $2n = 14$, 16, and 18 have been reported for species of the genus. The same numbers, plus higher ploidy levels of $2n = 36$, 45, 54, 60 and 64, have been found in *Sonchus*, further suggesting that it was derived from a *Launaea*-like stock.

The genus has no economic importance.

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11. **Hieracium** Linnaeus, Sp. Pl. **2**: 799. 1753; Gen. Pl. ed. 5. 350. 1754.

Perennial scapose or caulescent herbs, usually with a conspicuous indument (rarely glabrous). Leaves in a basal rosette and/or cauline, lanceolate, oblanceolate, entire, or dentate. Heads borne singly or in a panicle or cyme. Involucre of several (to two) series of herbaceous, imbricate bracts increasing in size toward the interior, often pilose with black hairs on the outer surface; receptacle flat to slightly convex, alveolate with membranaceous or ciliate margins, or naked. Corolla [sometimes subtubular] yellow, gold, or rarely orange-red in color, often with a tuft of hairs at the throat. Anthers with short sagittate auricles. Style branches thin, terete. Achenes terete, 4–10-ribbed, truncate at the apex, glabrous; pappus of simple setose bristles, white or brown. LECTOTYPE SPECIES: *H. murorum* L.; see Britton & Brown, Illus. Fl. No. U.S. ed. 2. **3**: 328. 1913. (Name from Greek *hierax*, hawk, because the Greeks believed that a similar plant, probably a species of *Crepis* [according to Zahn], was eaten by hawks to improve their eyesight.) — HAWK-WEED.

A cosmopolitan genus of between 150 (Bentham & Hooker) and 450 (Zahn) species which are usually arranged in four subgenera, each with numerous sections. The presence of recognizable apomictic populations has led to excessive splitting of species and elaboration of formally described taxa. Fortunately, the indigenous North American taxa appear to be sexually reproducing and have been more conservatively treated. Seven native species of subg. STENOTHECA (Monn.) Torrey & Gray, and at least four introduced species of subg. PILOSELLA (Schultz Bip.) Torrey & Gray occur in the southeastern United States.

The indigenous subg. STENOTHECA includes nonstoloniferous species with biseriate involucres and achenes with a smooth ring at the apex. Several species of this section hybridize in overlapping parts of their ranges. *Hieracium paniculatum* L., $2n = 18$, with its large, open panicles of heads frequents deciduous woodlands from Nova Scotia and southern Quebec to Michigan, south to Georgia and Alabama. It hybridizes with *H. scabrum* Michx., $2n = 18$, a morphologically similar plant with stiff, corymbose inflorescences of flower heads. The two are sympatric

over the entire range of *H. paniculatum*, but *H. scabrum* occurs farther westward to Oklahoma. *Hieracium Trailii* Greene (*H. Greenii* Porter & Britton), an inland species distributed from the mountains of Pennsylvania south through Georgia and Alabama, may also hybridize with *H. scabrum* in West Virginia (cf. Myers).

Several species included by Small in his *Manual of the Southeastern Flora* are now considered either to be conspecific with *Hieracium venosum* L., $2n = 18$, or to be hybrids between this and related taxa. According to Gleason & Cronquist, *H. marianum* Willd. (*H. argyraeum* Small) is either a variant of *H. venosum* or a hybrid between it and either *H. scabrum* or *H. Gronovii* L. Plants formerly known as *H. Scribneri* Small are probably hybrids between *H. venosum* and *H. paniculatum*. If *H. venosum* is circumscribed in its broadest sense, it can be characterized by the conspicuously maroon-outlined veins on the rosette of basal leaves. The species occurs in acid soils in open woods and clearings from southern Maine to southern Ontario south to Florida and Louisiana.

Hieracium Gronovii, also a plant of dry, open woods from Massachusetts to Michigan, south to Florida and Texas, is distinguished by its dense pubescence of trichomes less than 1 cm. in length. *Hieracium longipilum* Torrey is very similar, but has hairs 1–2 cm. long, and is midwestern in distribution, with a range extending from southwestern Ontario and Michigan, west to Minnesota and Nebraska, and south to Kansas, Louisiana, and eastern Texas. *Heracium megacephalon* Nash, our only species with a white pappus, is endemic to the southeastern pinelands of South Carolina, Georgia, and Tennessee.

At least four European species of subg. PILOSELLA, characterized by the presence of lateral stolons, an involucre of several series of bracts, and a dentate ring at the apex of the achene are established in our area. *Hieracacium Pilosella* L., $2n = 36, 39, 45, 54, 63$, a low plant with solitary yellow-flowered heads, now occurs in dry areas from Newfoundland to Quebec, to Oregon, and southeastward to North Carolina. The most easily recognized species of the subgenus, *H. aurantiacum* L., $2n = 30, 45$, has brilliant red-orange florets. Introduced as an ornamental garden plant, it has become a common, and often pernicious, weed in pastures, open woods, and along roadsides from Newfoundland to Ontario, south to Ohio and in the mountains to North Carolina. Two other introduced species, the yellow-flowered *H. pratense* Tausch., $2n = 36$, and *H. florentinum* All., $2n = 36, 45$, are very similar morphologically, generally having been distinguished by the pubescent leaf surface of *H. pratense*, and the glabrous one of *H. florentinum*. Myers recently has suggested from studies in the United States that either the two are the extremes of one polymorphic species or that extensive hybridization has occurred between them. *Hieracium pratense* frequents dry, disturbed soils across southern Canada and the United States from Michigan southeast to Georgia, while *H. florentinum* prefers calcareous areas from Newfoundland to Quebec and south to Wisconsin and North Carolina.

Numerous studies, the earlier ones of which have been excellently

summarized by Gustafsson (1946, 1947), have been made on the reproductive biology of various species of *Hieracium*. Later work has been done by Bergman, Battaglia, and Turresson & Turresson. There is apparently some correlation between the type of reproduction, the chromosome number, and the subgenera recognized by Zahn (e.g., asexual reproduction by means of stolons occurs only in species of subg. PILOSELLA). In both subg. PILOSELLA and subg. HIERACIUM, there is great variation in chromosome numbers, $2n = 18, 27, 30, 36, 42, 45, 54, 63$, to 90, and apomixis is found in both these subgenera. The presence of three types of apomixis is of unusual interest. In the first, diplospory, the megagametophyte is produced from a true megaspore mother cell that undergoes meiosis. The two nuclei of the first division unite to form a restitution nucleus. In plants with a diploid number of 27, the two transient nuclei have unequal numbers of chromosomes (usually 1 and 26 or 13 and 14). After the nuclei reunite, the original number of 27 is restored. The second type of apomixis is the development of an embryo from a nonmeiotic egg cell, and the third type is apospory, the formation of a megagametophyte from a somatic cell, in this case a cell from the megasporangium (nucellus). Embryos produced from reduced and nonreduced egg cells have been found within the same ovule, but the ameiotic one usually crushes the former.

In the subg. STENOTHECA, regular meiosis and a diploid number of $2n = 18$ predominates. It should be noted, however, that apomixis found in other subgenera is facultative, and some outbreeding usually also occurs (e.g., Skalinska).

Muller (1969) lists *Hieracium* as a genus that exhibits autotoxicity. Plants tend to form "fairy rings" as they grow out from the central area in which metabolic products presumably accumulate.

Several species of *Hieracium* are used in Europe as diuretics and tonics (cf. Fournier). *Hieracium Pilosella* has been used to combat Maltese fever because the plants contain umbelliferene, a 7-hydroxycoumarine, known to have antibiotic properties (see Duquénois *et al.* and Haag-Berrurier).

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12. **Prenanthes** Linnaeus, Sp. Pl. **2**: 797. 1753; Gen. Pl. ed. 5. 349. 1754, "*Prenantes*."

Erect caulescent perennial herbs with alternate, petiolate or clasping, lanceolate, sagittate or cordate, entire, serrate, dentate, or deeply parted leaves. Inflorescence paniculate or racemose, the heads nodding or, in a few species, ascending. Involucre narrow, composed of few, tiny exterior bracts, and long, lanceolate, stiff, scarious inner bracts; receptacle flat, naked. Corolla white, purple, violet, or ochre. Anthers with acute basal appendages; pollen echinolophate. Style long with terete branches. Achenes narrow, oblong, subterete, more or less 4- or 5-angled, inconspicuously ribbed, slightly constricted at the apex; pappus abundant, setose, brownish, reddish or yellow in color. (Including *Nabalus* Cass.) LECTOTYPE SPECIES: *P. purpurea* L.; see Cassini, Dict. Sci. Nat. Paris **34**: 96. 1825. (Name from Greek, *prenes*, nodding, and *anthos*, flower.) — RATTLESNAKE ROOT.

A genus of some 25 species native to Europe, eastern Asia and the Himalayas, and North America, with a single climbing species, *P. subpeltata* Stebbins, in the Virunga Mountains of Central Africa. Species from the Canary Islands, Java, and Venezuela, have also been referred to this genus, but all of these apparently belong to other genera (cf. Babcock).

Unfortunately, there is no modern revision of the genus which discusses its evolutionary history or the relationships of the Old and New World species. The North American species are being investigated by Milstead, who recognizes 12 species in the New World. These, and a few species of northeastern Asia constitute the subg. NABALUS (Cass.) Gray (treated as the genus *Nabalus* Cass. in Small's *Manual of the Southeastern Flora*). Although primarily of woodlands of the North Temperate Zone, seven species of this subgenus occur in the southeastern United States. *Prenanthes racemosa* Michx. and *P. Boottii* occur to the north of our area, and *P. alata* (Hooker) D. Dietr. and *P. sagittata* (Gray) A. Nelson occur in northwestern North America.

Our two most distinctive species both have sessile cauline leaves and racemose inflorescences, but differ in that *Prenanthes aspera* Michx. (*Nabalus aspera* (Michx.) Torrey & Gray), $2n = 18$, has a pubescent inflorescence with ascending heads, whereas *P. autumnalis* Walter (*P. virgata* Michx., *Nabalus virgatus* (Michx.) DC.) has a glabrous inflorescence of nodding heads. The former occurs in dry areas from Pennsylvania to Minnesota and South Dakota, south to Missouri, Arkansas, Kansas, and Louisiana, and the latter from the pine barrens of New Jersey southward on the Coastal Plain to Georgia and Florida.

Most of our species are part of a complex, the members of which have distinctly petiolate, more or less triangular, stem leaves. *Prenanthes trifoliolata* (Cass.) Fern. (*Nabalus trifoliolata* Cass.), $2n = 16$, around which these species cluster, has a yellowish pappus, extremely variable leaves, and, supposedly, a glabrous involucre of deltoid to ovate bracts as long as the pappus (cf. Cronquist in Gleason, *The New Britton & Brown*). The species is distributed across southern Canada from Newfoundland to Quebec, southward in oak and pine woods to Tennessee and Georgia. *Prenanthes Serpentaria* Pursh (*Nabalus Serpentaria* (Pursh) Hooker; incl. *P. integrifolius* Small), $2n = 16$, is said to be distinguished from the preceding species by its pubescent bracts that are lanceolate and shorter than the pappus. Since this taxon occurs on the Coastal Plain from Massachusetts to Florida, Alabama, and Mississippi (as well as inland to Pennsylvania), it may be an eastern ecological race of *P. trifoliolata*. Another taxon that may be an isolated member of the *P. trifoliolata-serpentaria* complex is *P. roanensis* (Chickering) Chickering (*Nabalus roanensis* Chickering), which was thought to be restricted to the mountains at the border of Tennessee and North Carolina but has recently been found in nearby Grayson County, Virginia (Uttal & Mitchell). These populations differ from surrounding ones in the conspicuous black pubescence on the involucral bracts. The last member of this complex, *P. cylindrica* (Small) E. L. Braun (*Nabalus cylindricus*

Small), is separated from the other taxa by the presence of sparse pubescence on the involucre. A rather uncommon taxon, it occurs in the mountains from North Carolina to Kentucky.

Similar in gross morphology to the species clustered around *Prenanthes trifoliolata*, but readily distinguished by its reddish-brown pappus, *P. alba* L. (*Nabalus albus* (L.) Hooker), $2n = 32$, is a tetraploid plant of moist woodlands from Quebec to Saskatchewan, south to South Dakota, Missouri, and Georgia. *Prenanthes crepidinea* Michx. (*Nabalus crepidineus* (Michx.) DC.) can be recognized by its numerous 20–35-flowered heads arranged in a corymbose panicle. Also a woodland species, it is more southern in distribution than *P. alba*, occurring from New York to Minnesota, south to Tennessee and Missouri.

Prenanthes altissima L. (*Nabalus altissimus* (L.) Hooker), $2n = 16$, has heads with fewer flowers (usually 5 or 6, not more than 8) and primary involucral bracts (5) than any other of our species. It occurs from Prince Edward Island and Quebec, south to Missouri, Louisiana, and Georgia. Although Fernald recognized var. *cinnamomea* Fern. in the southwestern part of its range, Milstead considered formal recognition to be unnecessary, since the southern populations constitute the ends of a north-south cline in pappus color.

Studies by Babcock suggested that *Prenanthes* is a relatively primitive genus in the Crepidinae (although not as unspecialized as some species of *Crepis*). He also considered the genus to have had formerly an intercontinental range (across the Bering land bridge) which was later restricted and led to the present pattern of isolated groups in Europe, southeastern Asia, and North America. The New World species appear to be most closely related to the Japanese species of subg. NABALUS.

On the basis of cytological studies, Babcock speculated that the primitive *Prenanthes* arose from an amphidiploid of a hybrid between parents with chromosome numbers of $n = 5$ and $n = 4$. However, with the exception of two, all of the species for which numbers are now known have $2n = 16$ or 32. Babcock, Stebbins, & Jenkins later suggested that there are two base numbers, 8 and 9, in the genus; and Milstead notes that in subg. PRENANTHES $x = 9$, while in subg. NABALUS, $x = 8$.

Although species of *Prenanthes* have no real economic importance, *P. alba* was used by the American Indians to "cure" snake bite. Investigations of the properties of the species have not yielded a substance which would seem to be effective as an antivenin. Plant extracts have also been used as a general tonic (cf. Millspaugh).

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13. **Lactuca** Linnaeus, Sp. Pl. 2: 795. 1753; Gen. Pl. ed. 5. 348. 1754.

Annual, biennial, or perennial glabrous or pubescent herbs with alternate cauline and/or basal leaves. Leaves entire, dentate, or pinnatifid. Inflorescence a panicle of numerous heads. Involucre composed of a few series of bracts increasing in size toward the inside and with scarious margins; receptacle flat, naked. Corolla yellow, blue, or white, the tube sometimes with a ring of long hairs at the summit. Anthers sagittate at the base, or with short setose-acuminate or acute auricles. Style branches, thin, short. Achenes flattened, ± 2-winged, beaked or beakless, but always terminated by a disc on which the pappus is borne, surface with a variable number of ribs; pappus setose or capillary (according to Stebbins, 1937, the bristles never more than four cells in thickness). (Including *Mulgedium* Cass., *Mycelis* Cass., and *Cicerbita* Wallr., in part.) LECTOTYPE SPECIES: *L. sativa* L.; see Britton & Brown, Illus. Fl. No. U.S. ed. 2. 2: 317. 1917. (*Lactuca*, classical Latin for lettuce, *L. sativa*, the name derived from *lac*, milk, referring to the the milky juice.) — LETTUCE, WILD LETTUCE.

A genus of some 50–90 species native to the temperate areas of Europe, Asia, Africa, and North and South America, with major centers of diversity in the Himalayas and the Middle East. There is no modern revision of the genus, and various authors (Bentham & Hooker, Hoffmann, Fernald) have recognized different subgenera or sections. Following Fernald's treatment (supplemented by work of Stebbins), we have nine species in two subgenera. Two additional species of a third subgenus, MYCELIS (Cass.) Babcock *et al.*, are adventive to the north of our area.

Subgenus LACTUCA (sect. *Scariola* DC.), which comprises species that have long achenes with soft beaks, is represented by two introduced and four indigenous species in the flora of the southeastern United States. *Lactuca canadensis* L., $2n = 34$, a very variable species (Fernald recognized four varieties) grows in disturbed grounds from Prince Edward

Island to Saskatchewan, south to Texas and Florida. *Lactuca graminifolia* Michx., $2n = 34$, with linear cauline leaves, occurs in dry habitats from North Carolina (according to Fernald also in the New Jersey pine barrens) south to Florida, west to Wisconsin and Colorado. The densely pubescent *L. hirta* Muhl. also grows in dry areas and open woods but is distributed over a much larger area, from Prince Edward Island, east to Ontario, south to Texas, Louisiana, Mississippi, and West Virginia. The fourth indigenous species, *L. ludoviciana* (Nutt.) Riddell, $2n = 34$, is a plant of grasslands and prairies primarily in the western United States but extending as far east as Missouri, Louisiana, and possibly Georgia.

The introduced European weeds *L. saligna* L., $2n = 18$, and *L. Serriola* L. (*L. Scariola* L.[7]), $2n = 18$, both prefer moist disturbed ground or waste areas but are also found in openings in woods and along streams. The former occurs from southern Canada, south to Georgia and New Mexico, and the latter is widely scattered in the United States. The leaves of both species are quite variable in shape, but those of *L. Serriola* are distinguished by a row of sharp teeth on the underside of the midrib.

The common garden lettuce, *Lactuca sativa* L., $2n = 18, 36, 36 + B$, is apparently not known as a wild plant but has escaped from cultivation in various parts of the world. Many authors think that *L. sativa* was derived from *L. Serriola* and that the two species should be considered conspecific. Anderson quotes unpublished work of M. Ownbey showing extensive introgression from garden lettuces into *L. Serriola*, "previously largely unsuspected because the hybrids and hybrid derivative mongrels were superficially so similar to wild lettuce and so unlike garden lettuce." If the two are united, *L. sativa* is the correct name.

Four species of subg. MULGEDIUM (Cass.) Gray (*Mulgedium* Cass.), comprising species that have achenes with a short, stout beak or none at all, occur in the Southeast. *Lactuca floridana* (L.) Gaertner, $2n = 34$, characterized by its blackish achenes and bright white pappus, can be found in wet woods from New York to Iowa, south to Texas and Florida. *Lactuca biennis* (Moench.) Fern., $2n = 34$, differing in its olive-colored achene and dirty-white pappus, ranges through most of the northern United States, south to Colorado, Tennessee, and North Carolina. *Lactuca pulchella* (Pursh) DC. was placed in subg. LACUASTRUM Gray by Fernald because its achenial beak is intermediate between that of subg. LACTUCA and subg. MULGEDIUM. Stebbins, however, treated it as subsp. *pulchella* (Pursh) Stebbins of *L. tatarica* (L.) C. A. Meyer, an Old World

[7] Both *Lactuca Serriola* L. (Cent. II. Pl. [Linn. Diss. 63]. 29. 1756; republished in Amoen. Acad. **4**: 328, 1759.) and *L. Scariola* L. (Sp. Pl. ed. 2, 1119. 1763), are in use as the name of this plant. As Shinners pointed out (Field & Lab. **17**: 175. 1949), *L. Scariola* must be considered an illegitimate substitute name for the earlier *L. Serriola*. *Lactuca Serriola* was properly published and is both valid and legitimate. Since Linnaeus gave exactly the same specific diagnosis for *L. Scariola* (1763) as for *L. Serriola* (1756) and cited the same synonyms, *Scariola* is clearly a substitute epithet for *Serriola*. As such, the combination *L. Scariola* is illegitimate, and the correct name of this species is *L. Serriola*. — C. E. WOOD, JR.

plant that Babcock *et al.* (1937) had put in subg. MULGEDIUM. This large-headed taxon is found in North America in open areas from Quebec to Alaska, south to Missouri, New Mexico, and California.

In a study of some American species of *Lactuca*, Babcock *et al.* found a mosaic of relationships, with some species more closely related to Old World species than to other American ones. *Lactuca floridana*, $2n = 34$, seemed to be related to two species of Asia Minor (*L. Marshallii* Stebbins, $2n = 16$, and *L. Bourgaei* Irish & Taylor in L. H. Bailey, $2n = 16$), and *L. canadensis*, $2n = 34$, appeared to be closest to an eastern Asiatic species (*L. formosana* Maxim., $2n = 18$). The nearest relative of *L. graminifolia* was postulated by these authors to be a nonscandent African species, such as *L. capensis*. Whitaker & Thompson have conducted experiments which seem to contradict the relationships proposed by Babcock *et al.* Experimental crosses between *L. floridana* and *L. canadensis* yielded viable F_1 and F_2 generations. The success of these crosses prompted Whitaker & Thompson to postulate that the parental species were descended from a common amphidiploid ancestor.

Lindqvist studied the relationships of the members of subg. LACTUCA and concluded that *L. Serriola, L. sativa, L. saligna, L. altaica* Fischer & Meyer, $2n = 18$, and *L. virosa* L., $2n = 16, 18$, should all be considered conspecific. The morphological character often used to separate the taxa involved is the position of the involucral bracts at the time of achene maturity. In both *L. sativa* and *L. altaica* the involucral bracts remain rigid and upright, while in the other taxa of this complex, the bracts reflex as the achenes ripen. Genetic studies have clearly shown that bract position is under the control of a single gene and that the condition of reflexed bracts is dominant over upright bracts (Lindqvist).

Stebbins and his colleagues have placed *Lactuca* in the *Prenanthes-Ixeris* line of the subtribe Crepidinae because of the morphological similarities of *Lactuca, Cicerbita* Wallr., and *Prenanthes*. Jeffrey's treatment agrees with this placement.

All of the subgenera of *Lactuca* contain groups of species with chromosomal base numbers of both 8 and 9. The presence of these two distinct base numbers throughout the genus led Babcock *et al.* to speculate that *Lactuca* is polyphyletic in origin, although they made no comment as to the possible ancestral stocks. In Africa there is an isolated group of species which are scandent herbs, morphologically unlike, and apparently unrelated to, other species of *Lactuca*. Stebbins thought that these herbs were derived from scandent species of *Prenanthes*, rather than from African or Asian species of *Lactuca*.

Numerous pollination, embryological, and physiological studies have been made of *Lactuca sativa* because of its importance as an economic plant (lettuce). Although cultivated plants are almost exclusively self-pollinated, cross-pollination can, and undoubtedly does, occur. The megagametophyte of this species is of the Polygonum-type (Jones), and apomixis apparently does not occur.

A recent conference on lettuce recognized 130 "varieties" (cf. Huyskes

& Rodenberg), but three basic types are usually seen: the cos, with loose spathulate leaves (i.e., garden lettuce); the cabbage (iceberg); and the lanceolate or columnella (Romaine). Types similar to these three were known to the ancient Persians at least 500 B.C. (Sturtevant). Lindqvist's experiments have shown that several of the differences in leaf shape are controlled by a multiallelic system in which entire leaves are recessive to the various degrees of lobing.

The "Grand Rapids" variety of lettuce has also become famous because its seeds were used by Flint & McAlister and later by Borthwick *et al.* for experiments on the effects of light on germination. The reversible red – far-red system of light interactions exhibited by these seeds has helped to formulate the modern phytochrome theory.

In Europe *Lactuca virosa* is grown commercially as a source of latex, lactucarium, which is used as a cough sedative.

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14. **Taraxacum** Wiggers, Prim. Fl. Hols. 56. 1780, nom. cons.

Perennial rosette herbs with scapose flowering stems arising from a straight or branched taproot. Basal leaves lanceolate to runcinate, entire, undulate, or doubly pinnatifid. Involucre of an inner series of connate, lanceolate bracts sometimes bifid at the apex, and an outer series of short, ovate bracts either appressed to the inner or reflexed; receptacle slightly convex, naked. Florets perfect (or functionally carpellate, the pollen abortive). Corolla yellow [violet, rose, or orange] with a dark band on the under side of the limb (ligule). Anthers sagittate at the base; pollen variable in shape (because of irregular meiosis), usually spherical, tricolporate, spinulose. Style branches thin, obtuse, variable in length. Achenes obconical, narrowing at the base, constricted at the apex, variously beaked, the beak terminating in a disc on which the pappus is borne; surface with 8 prominent ribs and up to 10 minor ribs, the upper half usually decorated with characteristic spines and knobs; pappus thin, soft, capillary, white. LECTOTYPE SPECIES: *T. officinale* Wiggers, typus cons. (Name probably of Arabic origin, applied by Theophrastus and Pliny to a yellow-flowered cichoriaceous plant, possibly a species of *Sonchus* L.) — DANDELION.

A now cosmopolitan genus indigenous to the North Temperate Zone. Estimates of the number of species vary from 6 (Bentham & Hooker) to over 1000 (Britton & Brown, ed. 2). This discrepancy in circumscription is caused by the predominance of asexual reproduction, which makes objective species delimitation almost impossible. Perhaps the most realistic treatment, and the one followed here, is that of Handel-Mazzetti (1907 & 1923) who recognized 63 species, which he ranked in 11 sections. European authors (e.g., Dahlstedt and van Soest) have since split the genus into numerous "species" and have erected sections that are difficult or impossible to correlate with those of Handel-Mazzetti. Although the geographical populations taxonomically treated as species by the

various authors are recognizable morphologically, it seems more meaningful biologically to group together those that appear to have very similar genomes and the possibility of interbreeding.

Sherff, in his treatment of the North American species of *Taraxacum*, followed the work of Handel-Mazzetti with the reduction of three species to synonymy and the addition of one neglected by the earlier author. Of the five species included in Sherff's study, two, both introduced, occur in the southeastern United States.

The common dandelion, *Taraxacum officinale*,[8] $2n = 16, 18, 22–26, 24, 33, 36, 37, 46–48$, of sect. TARAXACUM (sect. *Boreale* Handel-Mazzetti and in Sherff) is a native European weed now common all across southern Canada, Alaska, the United States, and in the uplands of Central and South America and the West Indies. Our second "species," the red-seeded dandelion, *T. laevigatum* (Willd.) DC.,[9] $2n = 16, 22, 24, 26, 32$, of sect. ERYTHROCARPUM Handel-Mazzetti, occurs in the southern part of Canada and in the United States from Maine to the Dakotas, south to Texas and Georgia. Although Fernald recognized 11 species in eastern North America, Gleason & Cronquist reduced the number to three, considering only *T. officinale, T. laevigatum*, and *T. ceratophorum* (Ledeb.) DC. as meaningful taxa.[10] The last occurs to the north and west of our area from New Hampshire and Massachusetts southwest to Mexico and California. The remaining species included in Sherff's treatment are found in northwestern North America, primarily in the Rocky Mountain area. Two additional segregate taxa, *T. lacistophyllum* (Dahlstedt) Dahlstedt and *T. disseminatum* Haglund have been identified by van Soest from specimens collected in Tennessee and Missouri respectively. *Taraxacum xanthostigma* Lindb., $2n = 24$, has been reported by Adams from Philadelphia, Pennsylvania.

The common dandelion, *Taraxacum officinale*, is easily distinguished from the red-seeded dandelion, *T. laevigatum*, by its greenish-brown achenes and, frequently, rather entire leaves. The achenes of *T. laevigatum* are red and the leaves are deeply lacerated. According to Berry, the red-seeded dandelion prefers sandier areas with little grass whereas the common one grows in more moist places, often with tall grass. Correll & Johnston, who recognize only *T. officinale*, comment, in *Manual of the Vascular Plants of Texas*, p. 1736, "The color of the achene varies from

[8] See Fernald (1948) for a clear explanation of why this is the correct name.

[9] There has been some debate as to whether the correct name for this species is *T. erythrospermum* Andrz. or *T. laevigatum*. Handel-Mazzetti, who examined the types of both names, considered them to be synonymous. Since *T. laevigatum* is the older name, it thus becomes the correct one. Shinners, however, decided that the American material did not agree with Willdenow's description of *T. laevigatum* and advocated the treatment of *T. erythrospermum* as a distinct species, a course previously followed in Britton & Brown, ed. 2 (*Illus. Fl. No. U.S.*), Fernald's *Gray's Manual*, and Small's *Manual*. In this article, as in Gleason & Cronquist (*The New Britton & Brown*), the circumscription of *T. laevigatum* is that of Handel-Mazzetti.

[10] See Cronquist in Gleason, New Britton & Brown Illus. Fl. Northeast. U.S. 3:532. 1952, for a discussion of the synonymy.

grayish or buffy to red-chestnut, but no other characters are correlated with this color and there seems to be no justification for recognition of *T. erythrospermum* as a separate entity."

Anatomical studies have been made primarily on the Asiatic *Taraxacum Kok-saghyz* Rodin, $2n = 16$, because of its use as a source of rubber during World War II. A review of the voluminous literature on this species can be found in Krotkov. The anatomy of *T. officinale* has been described by Gier & Burress, and that of *T. laevigatum* by Naylor. In both of these species a callus cylinder is formed outside the xylem if the crown of a plant is cut off. From this callus tissue, secondary vascular systems, which subsequently give rise to new rosettes, and ultimately, several independent plants, are initiated. (From this comes the frustration of gardeners who try to eliminate dandelions by cutting off the rosette of leaves.)

Apomixis has been reported for almost all species of *Taraxacum*, but most are still capable of some outbreeding, and this limited outbreeding may occasionally reintroduce new genetic material into apomictic populations. In the common dandelion, however, the amount of sexual reproduction during a given year seems to be almost negligible. Asexual seed production is possible from either an unreduced egg cell or one with a reconstituted diploid nucleus (cf. Nygren, Stork). Polyploidy has also been reported in both of our species and in numerous others of the genus. Diploid plants tend to have fairly constant pollen size and usually bloom for a short time early in the season. In contrast, polyploid plants have variably sized pollen grains, bloom early, and have a long flowering season (Fürnkranz). There seems to be no correlation within a species between the ploidy level and the geographic distribution, although plants with higher chromosome numbers are apt to grow in more disturbed areas.

The incompatibility system in sexually reproducing plants of *Taraxacum* is a four allele system with three of the alleles equal in the amount of expression ("strength") and all dominant to the fourth, as in *Crepis* L. and *Parthenium* L. (Okabe). The pollen incompatibility reaction is sporophytically controlled, with no incompatibility expressed in the style.

Part of the success of *Taraxacum officinale* as a ubiquitous weed is undoubtedly due to its germination system. Although some seeds germinate immediately, there is genetically controlled variation in germination time so that seedlings are produced continuously throughout the summer. Plants from achenes which germinate in the spring are robust by fall and flower the next spring; those from fall-germinated seeds are weak when winter sets in and frequently take up to three years to flower. Another reason for its success is undoubtedly its ability, because it reproduces by apomixis, to produce rapidly local, pure races well adapted to microhabitats within a heterogeneous habitat (Solbrig & Vuilleumier).

Although Bentham & Hooker considered *Taraxacum* to be related to *Leontodon* L., as had all previous authors, Stebbins placed them in separate subtribes, the former in the *Youngia-Ixeris* line of the Crepidinae, and the latter in the Leontodontinae.

Several species of *Taraxacum*, but primarily *T. officinale*, are used in European cookery. In some areas the unopened heads are pickled and used like capers. The ground, dried root is sometimes mixed with coffee. A wine is also made from macerated flower heads in a sugar solution inoculated with a fermentation culture. Dandelions are best known culinarily, however, for their leaves, which are eaten in salad or as a cooked vegetable.

Taraxacum is grown commercially in Europe for two additional purposes: the egg-shaped nectaries at the base of the style produce such an abundant amount of nectar (despite the presence of apomixis), that fields are planted near apiaries as a food source for the bees; and the taproots from several-year-old plants are dried and extracted for their content of inulin, which is used in the treatment of jaundice, constipation, and external sores.

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15. **Lapsana** Linnaeus, Sp. Pl. **2**: 811. 1753; Gen. Pl. ed. 5. 353. 1754.

Delicate, branching, glabrous or pubescent annual herbs arising from a slender taproot. Basal leaves few, oblanceolate to ovate, dentate to lyrately parted; stem leaves oblanceolate, entire, dentate or parted. Inflorescence a panicle (often flat-topped in ours) of heads borne on long peduncles. Involucre of small, ovate outer bracts forming a calyculus and a few stiff lanceolate inner bracts becoming swollen as the achenes mature [in some species, the bracts reflexed and forming a "star" when the achenes are shed]; receptacle ± flat, naked. Corolla yellow, the limbs (ligules) twisting together as they dry and wither. Anthers with sagittate bases. Style branches long, slender, terete. Achenes more or less cylindrical, slightly bent, constricted at both ends, glabrous, the pappus lacking. LECTOTYPE SPECIES: *L. communis* L.; see Britton & Brown, Illus. Fl. No. U.S. ed. 2. **3**: 306. 1913. (Name from Greek, *lapsane* or *lampsane*, a name given by Dioscorides to a vegetable apparently a species of *Raphanus*.) — NIPPLEWORT.

A genus of 9 species native to the extratropical regions of Europe, Asia, and northern Africa. Two species have been introduced into North America: the Chinese *Lapsana apogonoides* Maxim., $2n = 44$, in California, and the European *L. communis* L., $2n = 12, 14, 16$, which has spread across southern Canada and the United States to Oregon, and as far south as Missouri, Virginia, and Haywood County, North Carolina.

The only truly weedy member of the genus, *L. communis* is also adventive in at least Africa, Polynesia, the West Indies, and South America.

Bentham & Hooker allied *Lapsana* with *Apogon* Ell. (now included in *Krigia* L.), but Stebbins considered *Lapsana* (because of its lack of a pappus) to be a specialized offshoot of the *Youngia-Ixeris* line of the Crepidinae. Jeffrey indicated a similar relationship.

The several chromosome numbers of $2n = 12$, 14, and 16 reported for *Lapsana communis* suggest that apomixis may be involved, but only out-crossing and self-pollination have as yet been reported. As evidence of cross-pollination, Hegi listed numerous insect visitors, and J. Small elaborated on the pollinator-adapted stamen irritability. When stamens of this species are touched, the filament nearest the stimulus contracts and the entire anther tube faces the visitor as the style pushes out the pollen toward it. Yet, both Müller and Knuth assert that self-pollination must occur, since after anthesis the style branches diverge greatly and the stigmas undoubtedly become covered with pollen from neighboring florets when the heads "open in the morning and close at night."

Although not really important economically, Fournier included *Lapsana communis* in his list of medical plants because the expressed juice of the plants is used as a soothing lotion on sores and sensitive skin, particularly on the nipples of nursing mothers (hence the common name nipplewort). The young leaves are also occasionally eaten as salad greens.

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16. **Youngia** Cassini, Ann. Sci. Nat. **23**: 88. 1831.

Annual [biennial or perennial] herbs arising from a taproot [rhizome] and covered with scattered, multicellular trichomes. Leaves oblanceolate to lyrate, toothed or pinnatifid [entire]. Inflorescence of numerous small [to medium] [5–]10–20[–30]-flowered heads in a panicle [corymb]. Involucre of few, small outer bracts and 8 equal [6–12] longer, lanceolate inner bracts; receptacle slightly convex, naked. Corolla yellow. Anthers green, sagittate at the base. Style branches terete, yellow [in primitive species, branches flattened]. Achenes dorsiventrally compressed, unequally ribbed, with 3–5 ribs more prominent than others (in our species with

2–4 stronger), more or less spiny toward the apex, brown; pappus setose, white [to yellowish or cinereous], persistent. LECTOTYPE SPECIES: *Y. lyrata* Cass. = *Y. japonica* (L.) DC.; see E. B. Babcock & G. L. Stebbins, Carnegie Inst. Washington Publ. **484**: 5. 1937. (Name commemorating two Englishmen, one a poet, the other a physician, their identities not further revealed by Cassini.)

A genus of 28 species in six sections (cf. Babcock & Stebbins) native to Asia but with one weedy species, *Youngia japonica* (*Crepis japonica* (L.) Bentham), $2n = 16$, of sect. YOUNGIA (sect. *Euyoungia* Babcock & Stebbins), introduced and established in the United States in Maryland, North Carolina, Florida, and Louisiana. Indigenous from Japan and Korea to western China, northwestern India, the East Indies, New Guinea, and the Philippines, *Y. japonica* is widely naturalized in the tropics of the world. In the warmer parts of our area it seems to be spreading rapidly.

Although placed by most American authors (e.g., Small, Fernald, Rickett) in the genus *Crepis* L., Babcock & Stebbins assert that *Youngia japonica* belongs with a group of species in the phylogenetically distinct genus *Youngia*. Morphologically, the species of *Youngia* differ from those of *Crepis* in having numerous small heads, calyculate fewer-flowered involucres (i.e., with the small outer bracts mostly broad and closely imbricated), and compressed achenes with unequal ribbing (rather than columnar achenes with equal ribs as in *Crepis*). The similarities between some species of the two genera is, according to Babcock & Stebbins, the result of convergent evolution, not a reflection of close affinity. These authors also concluded that the two genera have distinct base chromosome numbers, 8 in *Youngia* and 5 in *Crepis*. Chromosome numbers of $2n =$ 10, 15, 16, 20, 24, and 32 have been reported for various species of *Youngia*, but it should be noted that the records of $2n = 15$ and 20 were from a species which also has individuals with $2n = 24$.

Data from morphology and anatomy have indicated that the closest relative of *Youngia* is *Ixeris* Cass. which has a similar type of calyculate involucre, pappus, corolla, anthers, and style branches (cf. Babcock & Stebbins).

In 1951, Babcock reported the occurrence of a new species of *Youngia*, *Y. americana* Babc., in Alaska. Hultén, however, in his recent *Flora of Alaska and Neighboring Territories* (1968) placed this species in the synonymy of *Crepis nana* Richardson var. *lyratifolia* (Turcz.) Hultén.

The genus appears to have no economic importance.

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17. **Crepis** Linnaeus, Sp. Pl. **2**: 805. 1753; Gen. Pl. ed. 5. 305. 1754.

Perennial [annual] herbs with rhizomatous rootstocks [taproots]. Leaves in a basal rosette and cauline, elliptic, lanceolate or oblanceolate, entire, dentate, or lyrately parted. Heads in a cymose arrangement [or flowering stems monocephalous]. Involucre of one row of more or less equal-sized bracts sometimes thickened at the base; receptacle flat, naked [fimbrillate, paleaceous, or membraneous at the edges of the achenial attachment points]. Corolla yellow [white]. Anthers sagittate at the base; pollen with ridges topped with spines. Style branches thin, terete. Achenes columnar, truncate [slightly beaked], surface glabrous with ribs of equal size; pappus setose, white to yellow in color. LECTOTYPE SPECIES: *C. tectorum* L.; see Britton & Brown, Illus. Fl. No. U.S. ed. 2. **3**: 325. 1919. (Name from Greek, *krepis*, sandal, probably in reference to the shape of the achene.) — HAWK'S BEARD.

A genus of about 200 species in three subgenera and 27 sections (cf. Babcock). Most of the species are native to the Old World, but the ten species of sect. PSILOCHAENIA (Nutt.) Babc. and *Crepis nana* Richardson and *C. elegans* Hooker, both of sect. IXERODOPSIS Babc., are indigenous to North America. These native American species are concentrated in the northwestern part of North America, and only *Crepis runcinata* (James) Torrey & Gray, which reaches Minnesota, and *C. nana* which extends to Newfoundland, range into the East. None of the native American species occurs in the southeastern United States, but species introduced from Eurasia are now established within our area.

Although a number of species have been reported from the southeastern United States, only two (neither included in Small's *Manual of the Southeastern Flora*) appear to be persistent. *Crepis capillaris* (L.) Wallr., $2n = 6$, of sect. PHAECASIUM Cass., a pubescent herb with a woody caudex and a fine setose pappus, is now established in areas from eastern Canada to Michigan, south (mostly in the mountains) to Virginia, North Carolina, and Tennessee. *Crepis pulchra* L., of sect. PHYTODESIA Babc., is a slender, glabrous, plant without a woody caudex and with achenes with a coarse, setose pappus. It is now found primarily in weedy areas in Virginia, North and South Carolina, Georgia, Mississippi, and Kentucky.

The taxon listed by Small, Fernald, and Rickett as *C. japonica* (L.) Bentham, is assigned here to the genus *Youngia* (*q.v.*) as advocated by Babcock and Babcock & Stebbins.

Other species recorded from the eastern United States by various authors include *C. tectorum* L., $2n = 8$, of sect. CREPIS (sect. *Mesophyllon* Babc.); *C. setosa* Haller f., $2n = 8$, of sect. NAMAUCHENES (Cass.) Babc.; *C. foetida* L., $2n = 10$, of sect. HOSTIA Moench. ex Babc., said by Small to occur in northwestern Florida and Georgia; *C. nicaeënsis*

Balbis ex Pers., of sect. PHYTODESIA Babc.; *C. biennis* L., $2n = 40$, of sect. BERINIA (Brignol) Babc.; and *C. vesicaria* L. subsp. *taraxacifolia* (Thuiller) Thellung ex Schinz & Keller, of sect. LEPIDOSERIS (Reichenb.) DC. It is uncertain whether any of these is to be regarded as an established member of our flora.

As a consequence of the intensive investigations of Babcock and his associates (1920–1947), *Crepis* is one of the most thoroughly documented genera of angiosperms, and Babcock's monograph stands as a landmark. His cytological analyses were among the first to demonstrate that species that are similar morphologically are also (usually) the most similar in gross chromosome structure and genetic make-up. Hybrid plants were shown to have chromosome complements that are karyotypically and genetically "hybrid." Babcock also documented the phenomenon of speciation by geographical isolation by showing that the genetic differences between species of *Crepis* are of the same type as, but simply of greater magnitude than, differences between isolated subspecies of a single species.

Chromosomal changes, both increases and decreases in number, as well as in gross morphology, apparently occurred repeatedly in the evolution of *Crepis*. The least specialized species seem to have a diploid number of $2n = 10$ and chromosomes with metacentric centromeres. The more advanced species have $2n = 8$ or $2n = 6$, and small, paracentric chromosomes. Babcock was even able to show that the chromosome number of $n = 4$ was derived from one of $n = 5$ by means of a translocation and (presumed) loss of a centromere. In the North American sect. PSILOCHAENIA a different type of chromosomal evolution, polyploidy, occurred. The species of this group, which have numbers ranging from $2n = 22$ to $2n = 88$, were apparently derived from ancestors which doubled (and later redoubled) in chromosome number after the hybridization of progenitors with haploid numbers of $n = 7 + n = 4$ or $n = 5 + n = 6$. Although apospory is uncommon in the genus, Babcock & Jenkins found that the higher polyploids are apomictic, the embryo being formed from a sporophytic cell. No species, however, seems to be obligately apomictic.

The less specialized species of *Crepis* are leafy, coarse, rhizomatous, perennial herbs with few flowering stems, large heads, and monomorphic achenes. Advanced species are smaller, tending toward a scapose habit, taprooted, small headed, and frequently with dimorphic achenes.

Gross morphological data combined with cytological analyses led Babcock to conclude that the extant species of *Crepis* stemmed from three major lineages which diverged from a common ancestral stock of *Dubyaea*-like morphology. The evidence suggested that the ancestral forms were present in Central Asia. Within the subtribe Crepidinae, *Crepis* is most similar to the *Ixeris-Youngia* phyletic line and to the *Hieracium-Tolpis* line (cf. Babcock, 1947).

The genus is economically unimportant.

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